
SYSTEMATICS OF XANTUSIID LIZARDS OF THE GENUS *LEPIDOPHYMA*

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ABSTRACT. Multivariate analyses of variation in 30 scale characters among 129 locality samples of members of the genus *Lepidophyma* (A. Duméril in Duméril and Duméril, 1851) identify the presence of 6 morphological groups in México below the latitude of 19°N. Univariate comparisons among the samples diagnose a total of 17 morphological species in the genus, 10 of which occur in southern México. Three species of *Lepidophyma* have broad (but discontinuous) geographic distributions: *L. flavimaculatum* A. Duméril in Duméril and Duméril, 1851 (Veracruz to Panamá), *L. smithii* Bocourt, 1876 (Guerrero to El Salvador), and *L. sylvaticum* Taylor, 1939 (Nuevo León to Veracruz). The other 14 members of the genus seem to have relatively small ranges, and 7 of these are known from only one or two localities. The greatest species diversity occurs in Oaxaca and Chiapas (10 species) and the northern Sierra Madre Oriental of Querétaro and San Luis Potosí (4 species).

RESUMEN. Un análisis multivariado de variación en 30 caracteres de escamas de 129 localidades con muestras de miembros del género de *Lepidophyma* (A. Duméril in Duméril y Duméril, 1851) identifica la presencia de 6 grupos morfológicos en México por debajo de la latitud de 19°N. Comparaciones univariadas entre todas las muestras diagnostican un total de 17 especies morfológicas en el género, 10 de las cuales se encuentran en el sureste de México. Tres especies de *Lepidophyma* tienen una amplia (pero discontinua) distribución geográfica: *L. flavimaculatum* A. Duméril in Duméril y Duméril, 1851 (Veracruz a Panamá), *L. smithii* Bocourt, 1876 (Guerrero a El Salvador) y *L. sylvaticum* Taylor, 1939 (Nuevo León a Veracruz). Los otros 14 miembros del género parecen tener áreas de distribución relativamente pequeñas y 7 de éstas se conocen únicamente de una o dos localidades. Las regiones con máxima diversidad de especies están en Oaxaca y Chiapas (10 especies) y el norte de la Sierra Madre Oriental en Querétaro y San Luis Potosí (4 especies).

INTRODUCTION

The living members of the family Xantusiidae range from the southwestern U.S. to Panamá and Cuba and comprise three genera: *Xantusia* Baird, 1859, *Lepidophyma* A. Duméril in Duméril and Duméril, 1851, and *Cricosaura* Gundlach and Peters in Peters, 1863. The majority of the diversity exists in the Middle American genus *Lepidophyma*, with 15 to 20 nominal species scattered from Nuevo León, México, to Panamá.

Like other xantusiid lizards, members of the genus *Lepidophyma* are secretive or reclusive and are seldom observed outside rock crevices, caves, and decaying tree stumps and logs. Most species are uncommon and/or difficult to collect. Their geographic distribution is spotty, with known localities often separated by considerable distances and represented by few museum specimens. The distributional gaps may be the result of several factors, including narrow habitat requirements, rugged topography, forest destruction, and inadequate field sampling. That many of the disjunctions may be real rather

than artifactual is suggested by high incidence of morphological divergence among the localities.

Since the description of *Lepidophyma* (Duméril and Duméril, 1851), a total of 25 taxa have been named in the genus, most of them based on one or two specimens from a single locality. Because many of the known localities are disjunct, represented by small sample sizes, and have various degrees of morphological differentiation, it remains unclear how many valid species exist in the genus, particularly in México (e.g., Flores-Villela, 1993; Liner, 1994; Smith, 1973).

In previous studies, we have delineated species of *Lepidophyma* in northeastern México (Bezy, 1984), Central America (Bezy, 1989), and within the cluster of species containing *L. gaigeae* Mosauer, 1936 (Bezy and Camarillo, 1992, 1997). In this paper we focus on delineating the morphologically diagnosable species found in México below the latitude of 19°N and synthesize the scattered information on the genus by providing summaries, diagnoses, and a key for all species of *Lepidophyma*.

MATERIALS AND METHODS

Data were taken for 31 scalation characters from a total of 1,420 specimens (including all holotypes) from 160 localities throughout the range of *Lepidophyma* (see Specimens Examined). As in previous studies (Bezy, 1984, 1989; Bezy and Camarillo, 1992, 1997), we used discrim-

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inant function analysis as an exploratory tool to visualize overall patterns of variation in these characters among localities. For these analyses, the individual locality samples constituted the *a priori* groups, but for clarity of presentation in the resulting plots, envelopes were constructed to enclose all individuals from larger geographic areas (usually countries of Central America and states of México). After delineation of the multivariate groups, the observed limits of variation of individual univariate characters were examined to identify discrete (nonoverlapping) differences among the locality samples and sample clusters. Thus, the species are diagnosed by univariate features and are not dependent on multivariate analyses. All analyses were performed with Systat 7.0 (SSPS, Chicago, IL, 60611 USA).

It is recognized that ratios violate the assumptions of a normal distribution and can influence the results of multivariate analyses, particularly principal components analyses (e.g., Atchley et al., 1976). In analyses of data, we found the results of discriminant analyses that used ratios generally to be congruent with those from analyses based on the residuals from regression of the morphometric variables on snout-vent length (SVL). Despite their statistical drawbacks, we employ ratios because we found them to be more useful in recognizing and diagnosing morpho-species.

We embrace the evolutionary species concept (e.g., Wiley, 1978) and its operational equivalent, the phylogenetic species (e.g., Cracraft, 1983). We thus recognize as separate species any locality sample or group of samples that has 1 or more discrete difference(s) from each of the other samples or groups (i.e., for each pairwise comparison there are 1 or more characters for which the observed limits of variation do not overlap). In most cases these morpho-species are composed of disjunct populations and probably are not united by gene flow. Whether they actually represent monophyletic groups of isolated populations is difficult to determine with the quantitative scale features utilized in this study, but the question is being addressed by phylogenetic analyses of mitochondrial DNA sequences combined with morphology (R.L. Bezy and collaborators, unpublished).

In our analyses of variation, we make three exceptions to the requirement that species of *Lepidophyma* have discrete (nonoverlapping) differences in morphology. Two of the exceptions involve species pairs that are 100% diagnosable by univariate differences in areas where they occur in sympatry, but that have a small overlap in the observed limits of variation for geographically distant localities (where a combination of 2 univariate characters serves to distinguish the species). This is the operational equivalent of considering that "biological species" are a subset of "evolutionary species." The third exception involves 2 allopatric species which have slight overlap in 2 morphological characters but have discrete differences in karyotypes throughout their ranges.

We have chosen not to recognize subspecies in the genus because of the large number of geographically isolated samples with morphological features that are statistically different but that overlap the observed limits of variation in other samples.

STANDARD CHARACTERS

The standard data taken on all specimens consist of 31 scale characters: 21 meristic, 9 mensural, and 1 presence/absence. We employ the scale terminology of Savage (1963) rather than that of Smith (1973) in that we consider the parietals to be the scales on each side of the

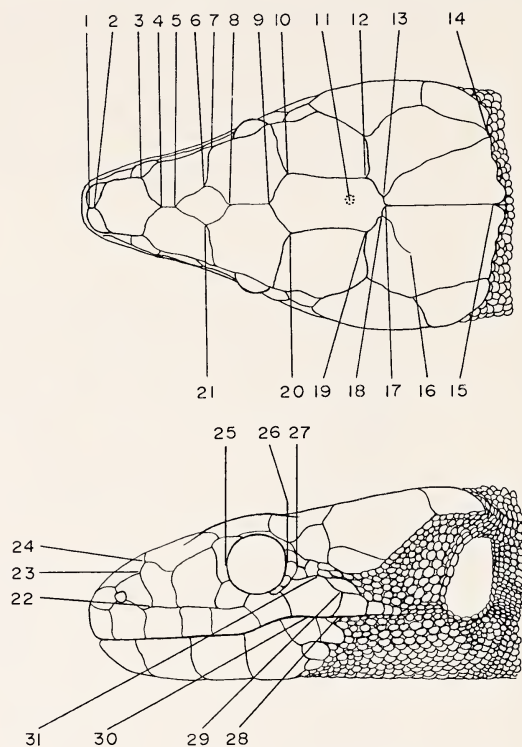


Figure 1 Dorsal and lateral views of the head of a generalized specimen of *Lepidophyma*. Numbered points were used in scale measurements and counts (see Materials and Methods).

interparietal rather than the pair posterior to it. In the descriptions below, "at midbody" indicates that the count was made midway between the gular fold and the vent, above a point corresponding to half the total number of transverse rows of ventrals.

Pretympanics (PTMP). The minimum number of small scales (pretympanics) separating the postoculars (Fig. 1: 26, 27) from the second postorbital supralabial (sum of right plus left side of head). The second postorbital supralabial (Fig. 1: 28) is usually the seventh and is the second labial scale posterior to the eye that does not enter the orbital ring of scales. Supralabial scales are skirted and not included in the count. For example, there are a minimum of 4 pretympanics in Fig. 1, between points 27 and 29.

Gulars (GUL). The number of small scales (gulars) along the ventral midline between the posterior gular fold and the second pair of infralabials (Fig. 2, between points A and B).

Gulars Contacting First Infralabials (GC1IL). The number of gulars in contact medially with first pair of infralabials. (Fig. 2, 1 gular at point C).

Dorsals (DOR). The number of scales along the mid-dorsal line between the posterior edge of the postparietals and a point directly above the vent.

Dorsals Between Paravertebral Rows (DBPVR). The minimum number of dorsal scales separating the rows of large paravertebral tubercles (at midbody; Fig. 2, 5 dorsals separate tubercles D and F)

Dorsals Along Paravertebral Row (DAPVR). The num-

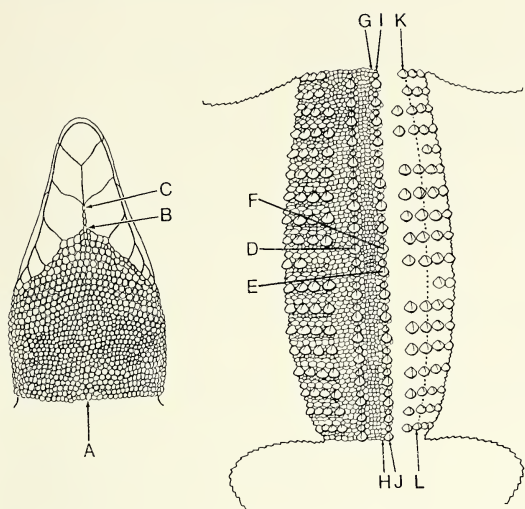


Figure 2 Ventral view of head and dorsal view of body (axilla to groin) of a generalized specimen of *Lepidophyma*. Lettered points were used in scale counts (see Materials and Methods).

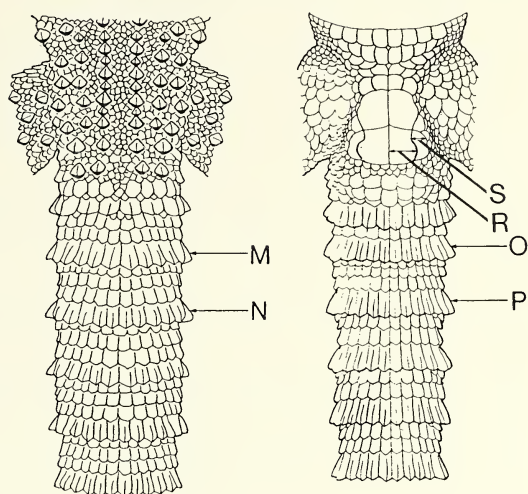


Figure 3 Dorsal (left) and ventral (right) views of the pre-anal area and the proximal portion of the tail of a generalized specimen of *Lepidophyma* with characters indicated by letters (see Materials and Methods).

ber of dorsals (from above the axilla to above the groin) in the row immediately above (i.e., medial to) the paravertebral tubercle row (Fig. 2, G to H).

Dorsals Between Paravertebral Tubercles (DBPVT). The number of middorsal scales equivalent to the distance between 2 consecutive large tubercles (largest size class) within the paravertebral row (at midbody; Fig. 2, the distance between tubercles E and F is equal to 4 dorsals).

Large Paravertebral Tubercles (PVTL). The number of large tubercles (largest size class) in the paravertebral row (from above the axilla to above the groin; Fig. 2, between I and J there are 18 large tubercles).

Paravertebral Row (PVR). The total number of scales (all sizes) in the paravertebral row (from above the axilla to above the groin; Fig. 2, there are 54 scales between I and J).

Paravertebrals, Small (PVS). The number of scales (from above the axilla to above the groin) in the paravertebral row that are shorter than 1.5 dorsal scales.

Paravertebrals, 1.5 (PVT1.5). The number of scales (from above the axilla to above the groin) in the paravertebral row that are equal to or longer than 1.5 middorsal scales.

Paravertebrals, 2 (PVT2). The number of scales (from above the axilla to above the groin) in the paravertebral row that are equal to or longer than 2 middorsal scales.

Paravertebrals, 3 (PVT3). The number of scales (from above the axilla to above the groin) in the paravertebral row that are equal to or longer than 3 middorsal scales.

Lateral Tubercle Rows (LTR). The number of large tubercular scales (largest size class) on the side of the body between the axilla and groin. The count is made along a longitudinal line that is parallel to the paravertebral row and that passes through the second large lateral tubercle below the paravertebrals (Fig. 2, there are 16 tubercle rows along line K to L).

Dorsal Interwhorls (IWD2). The maximum number of annuli of small scales separating the second from the third

whorl of enlarged caudal scales (at middorsum; Fig. 3, three dorsal interwhorls between M and N).

Ventral Interwhorls (IWV2). The minimum number of ventrally complete annuli of small scales separating the second from the third whorl of enlarged caudal scales (Fig. 3, 3 complete ventral interwhorls between O and P).

Ventrals, Longitudinal (VL). The number of transverse rows of large ventral scales between gulars and the vent, including the preanals.

Ventrals, Across (VA). The number of longitudinal rows of ventrals across midbody. Longitudinal rows were excluded if (at midbody) they contain 2 more scales that are in contact with a single scale of the medially adjacent longitudinal row of ventrals.

Femoral Pores (FPT). The total number of pores (right plus left femoral surface). In females and juveniles some or all of the pores may be vestigial or "undeveloped" (marked by shallow depressions rather than discrete glandular openings). On all specimens the counts include both "developed" and "undeveloped" pores.

Fourth Toe Lamellae (FTL). The number of scales along the ventral midline of the fourth toe between the base and the claw.

Divided Fourth Toe Lamellae (FTLD). The number of scales under the fourth toe with midventral sutures.

Parietal Spot (PS). The presence (1) or absence (0) of a pale spot on the interparietal scale. The spot marks the approximate position of the parietal foramen (which may be roofed over by bone in adults) and is located along the dorsal midline, usually in the posterior half of the scale (Fig. 1, point 11).

Prefrontal Length (RPFL). Ratio of the length along the midline of the lateral prefrontal (Fig. 1, points 4 to 6) divided by the length along the lateral border of the lateral prefrontal (Fig. 1: 3 to 7).

Median Prefrontal Length (RML). Ratio of the length of the median prefrontal (Fig. 1: 5 to 8) divided by the length of the midline suture of frontals (Fig. 1: 8 to 9). Specimens lacking a median prefrontal were scored as 0.

Table 1. Variation in 31 scale characters for 17 species of *Lepidophyma*. In each cell, the upper number is the mean, the middle is the standard error, and the lower are the observed limits of variation. Sample size (N) is given below the species name.

Species	PTMP	GC1L	GUL	DOR	DBPVR	DAPVR	DBPVT	PVTL	PVR	PVS	PVT1.5	PVT2	PVT3	LTR	IWD2	IWV2
<i>L. dontomasi</i>	2.1	0.3	32.1	140.3	3.62	70.6	2.31	20.2	51.0	27.6	23.4	12.4	0.0	52.2	2.0	1.0
29	0.09	0.09	0.30	1.06	0.073	0.86	0.107	0.50	0.72	1.29	0.78	0.65	0	0.62	0	0
<i>L. gaigae</i>	1-4	0-1	28-35	128-149	3.0-4.0	62-83	1.0-3.5	15-26	43-61	11-45	15-36	6-20	0	47-60	2	1
177	3.5	0.2	36.801	136.0	4.12	66.0	2.72	10.8	54.4	39.1	15.2	4.2	0.0	51.8	2.1	1.9
<i>L. louei</i>	0.09	0.03	0.17	0.449	0.027	0.41	0.043	0.43	0.50	0.94	0.55	0.33	0.02	0.47	0.02	0.02
16	2-7	0-2	28-44	121-151	3.0-5.0	53-83	1.0-3.5	0-26	30-74	8-72	0-38	0-18	0-3	39-73	2-3	1-2
<i>L. lowei</i>	2.6	0.0	34.4	163.8	3.31	87.9	1.63	24.6	51.9	26.6	25.3	23.4	0.4	29.0	2.1	1.0
16	0.18	0	0.32	1.00	0.101	1.21	0.148	0.55	0.90	1.33	0.71	0.67	0.16	0.26	0.06	0.00
<i>L. radula</i>	2-4	0	32-37	158-170	3.0-4.0	82-96	1.0-2.5	21-27	45-60	18-38	21-32	18-27	0-2	28-31	2-3	1
1	3.0	0.0	32.0	135.0	2.50	69.0	1.00	24.0	46.0	18.0	28.0	23.0	1.0	24.0	2.0	1.0
<i>L. smithii</i>	3	0	32	135	2.5	69	1	24	46	18	28	23	1	24	2	1
397	2.8	0.8	52.2	198.2	3.95	98.2	3.12	17.2	51.8	19.1	32.7	28.2	17.2	17.6	3.0	2.0
<i>L. tarascae</i>	0.06	0.05	0.20	0.68	0.301	0.50	0.027	0.10	0.34	0.4	0.15	0.21	0.11	0.08	0.014	0.01
4	2-7	0-4	44-61	162-224	3.0-5.5	74-121	1.5-4.5	14-25	35-69	6-40	25-44	17-38	13-27	15-22	1-4	1-2
4	4.0	1.0	41.8	149.8	2.75	78.3	2.50	16.5	45.5	14.8	30.8	25.3	16.0	18.8	2.3	2.0
<i>L. lineri</i>	0	0.41	0.75	3.30	0.25	3.33	0	0.5	1.44	1.44	0.25	1.11	0	2.10	0.25	0
3	4	0-2	40-43	145-159	2.0-3.0	74-88	2.5	16-18	42-49	11-18	30-31	23-28	16	16-25	2-3	2
<i>L. mayae</i>	3.0	0.0	51.5	181.5	3.67	88.3	2.67	18.0	49.0	16.3	32.7	25.0	15.7	23.7	3	2.0
16	0	0	0.50	2.50	0.333	2.33	0.167	0.58	3.1	1.45	1.86	1.16	1.33	0.33	0	0
<i>L. pajapanense</i>	3	0	51-52	179-184	3.0-4.0	86-93	2.5-3.0	17-19	43-53	14-19	29-35	23-27	13-17	23-24	3	2
22	1.9	0.1	41.4	174.8	4.13	79.7	0.29	34.5	50.5	8.9	42.0	29.2	1.7	37.4	3.9	2.1
16	0.06	0.07	0.43	1.96	0.072	1.50	0.215	2.06	1.14	1.02	1.23	1.80	0.90	0.83	0.10	0.07
<i>L. tuxtlae</i>	1-2	0-1	38-44	162-188	4.0-5.0	72-91	0.0-3.0	21-46	41-57	29-42	29-49	14-40	0-11	33-46	3-4	2-3
97	7.5	0.2	39.2	165.1	4.18	70.0	0.12	43.5	44.0	2.7	41.3	26.5	0.0	40.0	3.1	2.0
<i>L. chicaoense</i>	0.28	0.08	0.50	1.46	0.078	1.14	0.033	0.89	0.72	0.49	0.88	1.23	0.05	0.44	0.072	0
4	6-10	0-1	35-43	152-175	4.0-5.0	59-82	0.0-0.5	39-51	37-49	0-8	34-49	15-40	0-1	36-43	3-4	2
<i>L. lipetzi</i>	5.5	1.6	42.8	172.3	4.08	79.7	0.24	39.5	45.2	5.1	40.1	32.5	1.7	34.1	3.6	2.1
2	0.10	0.08	0.27	0.86	0.045	0.61	0.028	0.41	0.39	0.42	0.35	0.56	0.28	0.19	0.06	0.02
4	4-9	0-4	37-52	150-190	3.0-5.0	69-98	0.0-0.9	30-49	37-55	0-18	31-49	13-27	0-15	30-40	2-5	2-3
<i>L. lipetzi</i>	7.8	1.3	54.5	181.8	3.88	92.8	3.00	22.8	62.3	24.8	37.5	21.8	2.00	31.5	3	2.0
2	0.25	0.3	0.65	3.47	0.125	2.29	0.408	1.11	2.87	3.68	3.30	3.04	1.16	0.29	0	0
2	7-8	1-2	53-56	177-192	3.5-4.0	87-98	2.0-4.0	21-26	57-70	14-30	31-45	13-27	0-4	31-32	3	2
2	7.0	0.0	49.0	178.0	4.00	90.5	2.00	27.0	59.5	19.0	40.5	28.0	1.0	32.5	3.5	2.0
<i>L. lipetzi</i>	1.00	0	3.00	1.00	1.00	2.50	1.000	4.00	0.50	1.00	0.50	0	0.2	0.50	0.50	0.00
2	6-8	0	46-52	177-179	3.0-5.0	88-93	1.0-3.0	23-31	59-60	18-20	40-41	28	0-2	32-33	3-4	2

Table 1. Continued.

Species	PTMP	GC1IL	GUL	DOR	DBPVR	DAPVR	DBPVT	PVTL	PVR	PVS	PVT1.5	PVT2	PVT3	LTR	IWD2	IWV2
<i>L. flavimaculatum</i> 433	7.2 0.06 2-11	0.5 0.03 0-3	47.5 0.13 40-55	201.1 0.46 170-225	4.38 0.023 3.0-6.0	88.5 0.29 67-118	3.15 0.031 0.5-4.5	17.798 0.11 13-27	55.9 0.25 41-74	18.4 0.28 6-44	37.6 0.22 24-52	24.4 0.18 17-38	14.1 0.17 1-24	27.497 0.09 23-33	3.7 0.02 3-4	2.0 0.00 1-2
<i>L. reticulatum</i> 65	5.7 0.14 4-8	1.1 0.10 0-3	47.5 0.25 44-54	213.9 0.65 193-229	4.26 0.048 3.5-5.0	103.1 0.66 88-113	3.92 0.076 1.0-5.0	16.7 0.16 15-23	62.1 0.51 52-72	23.3 0.79 10-43	38.7 0.57 29-47	25.4 0.42 17-32	14.1 0.25 6-18	30.6 0.17 28-33	4.0 0.05 3-5	2.0 0 2
<i>L. micropholis</i> 31	1.5 0.13 0-2	0.6 0.12 0-2	60.9 0.76 55-72	241.1 1.06 230-251	5.60 0.130 4.0-7.0	123.2 1.44 107-140	4.84 0.078 4.0-6.0	16.3 0.35 15-26	68.0 1.48 52-85	35.5 1.75 17-56	32.4 0.68 25-41	26.6 0.84 13-20	16.2 0.28 13-20	30.2 0.31 27-35	3.7 0.09 3-4	2.0 0 2
<i>L. occulor</i> 11	2.1 0.09 2-3	0.0 0 0	63.2 1.23 58-71	230.5 2.89 213-242	4.41 0.251 3.0-5.5	112.2 2.28 100-122	4.09 0.163 3.0-5.0	15.8 0.26 15-17	60.2 2.13 49-69	29.9 2.18 18-39	30.3 0.81 23-33	30.3 0.38 29-33	18.5 0.89 15-23	22.5 0.51 22-25	3 0 3	2.0 0 2
<i>L. sylvaticum</i> 112	2.0 0.07 0-4	0.6 0.06 0-3	46.7 0.33 40-56	181.0 1.24 150-217	4.04 0.069 2.5-5.0	92.5 7.2 77-113	2.86 0.077 1.0-4.5	18.7 0.46 15-39	52.7 0.74 39-73	22.9 0.90 7-56	29.7 0.39 17-37	21.4 0.44 15-34	9.69 0.57 0-18	28.7 0.58 15-38	3.01 0.04 2-4	2.0 0.01 1-2

Table 1. Extended.

Species	VL	VA	FPT	FTL	FTLD	PS	RPFL	RML	RMW2	RNL	RAPPSL	RPNH	RPOL	RSLH	RPAW
<i>L. dorttomasi</i> 29	32.3	10.1	19.2	20.3	5.0	1.00	0.838	2.652	2.211	0.198	0.032	0.790	0.174	0.959	0.592
	0.19	0.07	0.21	0.20	0.20	0	0.013	0.115	0.060	0.007	0.015	0.014	0.006	0.022	0.017
	30-34	10-12	17-21	18-22	3-7	1	0.68-0.95	1.69-4.49	1.71-2.96	0.14-0.31	0-0.29	0.68-0.94	0.12-0.27	0.77-1.16	0.44-0.77
<i>L. gaigeae</i> 177	35.1	10.0	33.2	25.6	10.4	1.00	0.385	0.10	0.228	0.196	0.051	0.779	0.195	0.742	0.465
	0.08	0	0.18	0.108	0.18	0	0.011	0.02	0.032	0.004	0.009	0.009	0.003	0.008	0.008
	33-38	10	28-29	22-30	6-17	1	0.00-0.81	0-1.24	0-1.98	0.08-0.36	0-0.67	0.63-1.65	0.09-0.39	0.40-1.12	0.20-0.78
<i>L. louei</i> 16	33.5	10.0	24.4	20.8	4.4	1.00	0.773	2.162	2.118	0.208	0	0.796	0.205	0.887	0.48
	0.18	0	0.52	0.25	0.44	0	0.021	0.263	0.129	0.01	0	0.013	0.010	0.037	0.021
	33-35	10	22-31	19-23	3-7	1	0.59-0.90	1.05-4.33	0.89-2.92	0.12-0.28	0	0.70-0.90	0.13-0.28	0.61-1.10	0.36-0.67
<i>L. radula</i> 1	33.0	10.0	20	20.0	6.0	1.00	0.869	4.077	2.495	0.214	0	0.697	0.202	0.782	0.568
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	33	10	20	20	6	1	0.87	4.08	2.50	0.21	0	0.70	0.20	0.78	0.57
<i>L. smithii</i> 397	36.1	10.0	21.2	25.4	6.5	0.06	0.677	0.869	1.128	0.144	0.037	0.779	0.177	0.832	0.661
	0.06	0.01	0.15	0.09	0.12	0.014	0.021	0.034	0.039	0.003	0.007	0.003	0.002	0.008	0.009
	33-39	10-12	15-30	20-29	2-13	0-1	0.25-6.25	0-2.62	0-2.74	0.00-0.32	0-1.04	0.62-1.01	0.09-0.42	0.37-1.29	0.33-1.35
<i>L. tarascae</i> 4	35.0	10.0	16.3	22.5	2.8	0.00	0.397	0	0	0.134	0	0.926	0.296	0.754	0.622
	0.71	0	0.85	0.29	1.11	0	0.059	0	0	0.022	0	0.059	0.051	0.03	0.072
	34-37	10	14-18	22-23	1-6	0	0.29-0.50	0	0	0.07-0.18	0	0.76-1.02	0.19-0.44	0.69-0.83	0.41-0.71
<i>L. lineri</i> 3	36.3	10.0	16.3	23.7	5.3	0.00	0.293	0.124	0.281	0.137	0	0.828	0.155	0.903	0.746
	0.67	0	0.33	0.67	2.03	0	0.051	0.030	0.042	0.02	0	0.005	0.007	0.047	0.095
	35-37	10	16-17	23-25	2-9	0	0.24-0.34	0.09-2.16	0.24-0.32	0.12-0.16	0	0.82-0.83	0.15-0.16	0.86-0.95	0.56-0.87
<i>L. mayae</i> 16	36.6	10.0	32.3	25.1	14.8	1.00	0.718	1.493	2.485	0.183	0	0.823	0.193	0.913	0.501
	0.24	0	0.47	0.42	0.65	0	0.022	0.074	0.239	0.014	0	0.034	0.017	0.042	0.032
	35-38	10	29-35	23-28	10-19	1	0.57-0.89	1.09-2.16	1.69-5.46	0.12-0.33	0	0.70-1.27	0.11-0.31	0.71-1.35	0.38-0.77
<i>L. pajapanense</i> 22	36.7	10.1	33.4	28.5	14.2	1.00	0.812	1.729	2.713	0.167	0.006	0.763	0.222	0.506	0.534
	0.18	0.09	0.33	0.24	0.49	0	0.015	0.116	0.169	0.01	0.005	0.01	0.007	0.033	0.018
	35-38	10-12	30-36	26-30	10-18	1	0.70-1.00	1.00-2.81	1.46-4.26	0.10-0.28	0-0.10	0.69-0.86	0.13-0.28	0.32-0.88	0.38-0.69
<i>L. tuxtlae</i> 97	39.7	10.0	24.5	25.8	16.297	1.00	0.735	1.209	2.679	0.11	0.023	0.732	0.226	0.539	0.82
	0.13	0.02	0.20	0.15	0.21	0	0.009	0.046	0.067	0.005	0.013	0.005	0.004	0.009	0.012
	37-43	8-11	18-29	22-29	12-21	1	0.48-1.05	0-3.15	0-4.74	0.04-0.29	0-0.99	0.61-0.85	0.12-0.33	0.32-0.77	0.56-1.12
<i>L. chicoasense</i> 4	38.3	12.0	35.5	36.0	13.3	1.00	0.87	1.508	2.469	0.159	0	0.757	0.172	0.475	0.415
	0.25	0	1.19	0.41	1.11	0	0.031	0.214	0.11	0.014	0	0.014	0.005	0.042	0.026
	38-39	12	33-38	35-37	11-16	1	0.78-0.91	1.02-2.0	2.20-2.67	0.14-0.20	0	0.74-0.80	0.16-0.18	0.38-0.57	0.37-0.49
<i>L. lipetzi</i> 2	37.5	11.5	36.5	27.5	12.5	1.00	0.813	1.243	3.270	0.176	0.105	0.962	0.162	0.441	0.48
	1.5	0.50	1.50	0.50	1.50	0	0.015	0.056	0.267	0.016	0.105	0.213	0.001	0.041	0.084
	36-39	10-12	35-38	27-28	11-14	1	0.80-0.83	1.19-1.30	2.99-3.55	0.16-0.19	0-0.21	0.75-1.118	0.16	0.40-0.48	0.40-0.57

Table 2. Variation in 10 scale characters among samples of group S of *Lepidophyma*. The observed limits of variation are followed by the mean (in parentheses).

	N	FPT	LTR	GUL	DOR
<i>L. tarascae</i>					
Michoacán	4	14–18 (16.8)	16–25 (18.8)	40–43 (43.8)	145–159 (149.8)
<i>L. lineri</i>					
Oaxaca					
El Pacífico	2	16	23–24 (23.5)	51–52	179–184 (181.5)
Alemania	1	17	24	—	—
<i>L. smithii</i>					
Veracruz	1	20	18	51	198
Guerrero	17	26–30 (27.3)	15–19 (16.7)	50–57 (53.6)	176–194 (185.6)
Oaxaca	78	15–26 (20.2)	15–20 (17.8)	44–59 (52.0)	162–213 (191.4)
Puerto Escondido	2	15–16 (15.5)	17–18 (17.5)	44–49 (46.5)	173–189 (181.0)
Tehuantepec	30	16–26 (21.5)	15–20 (17.4)	44–57 (51.0)	164–209 (187.1)
Tapanatepec	20	16–21 (19.3)	15–19 (16.8)	49–59 (54.4)	190–213 (200.8)
Chiapas	150	16–27 (21.1)	16–22 (17.9)	44–58 (51.9)	182–224 (202.7)
Tonalá	9	16–22 (18.9)	17–18 (17.4)	46–58 (52.3)	189–219 (204.1)
Escuintla	136	17–27 (21.3)	16–22 (18.0)	44–58 (51.8)	182–224 (202.5)
Guatemala	54	17–24 (20.8)	15–21 (17.4)	46–61 (52.9)	173–217 (198.3)
El Salvador	3	16–24 (18.7)	16–18 (17.0)	46–51 (48.3)	196–208 (203.0)

Median Prefrontal Width (RMW2). Ratio of the width of the median prefrontal (Fig. 1: 6 to 21) divided by height of the second postorbital supralabial (Fig. 1: 28 to 29). Specimens lacking a median prefrontal were scored as 0.

Nasal Length (RNL). Ratio of the length of the midline suture of the nasals (Fig. 1: 1 to 2) divided by length of the midline suture of the postparietals (Fig. 1: 15 to 17).

Anomalous Postparietal Suture Length (RAPPSL). Ratio of the total length of all anomalous sutures on both postparietals (Fig. 1: 13 to 14 plus 16 to 18) divided by length of the midline suture of postparietals (Fig. 1: 15 to 17).

Postnasal Height (RPNH). Ratio of the height of the postnasal (Fig. 1: 22 to 23) divided by height of the anterior loreal (Fig. 1: 22 to 24).

Postocular Length (RPOL). Ratio of the maximum length of the postoculars (Fig. 1: 26 to 27) divided by length of the orbit (Fig. 1: 25 to 26).

Supralabial Height (RSLH). Ratio of the height of the second postorbital supralabial (Fig. 1: 28 to 29) divided by height of the first postorbital supralabial (Fig. 1: 30 to 31). The first postorbital supralabial is usually the sixth and is the first labial scale posterior to the eye that does not enter the orbital ring of scales.

Preanal Width (RPAW). Ratio of the maximum width of the lateral posterior preanal (Fig. 3: S) divided by maximum width of the median posterior preanal (Fig. 3: R).

AUXILIARY CHARACTERS

The following 5 additional characters were used for comparisons among the samples in one of the clusters (group S).

Median Prefrontal (M). Presence (1) or absence (0) of a median prefrontal.

Median Prefrontal Contact (MC). Presence (1) or absence (0) of a contact between the median prefrontal and the frontal. Specimens lacking a median prefrontal were scored as 0.

Median Prefrontal Length 2 (RML2). Ratio of the

length of the median prefrontal (Fig. 1: 5 to 8) divided by length of the midline suture of postparietals (Fig. 1: 15 to 17). The character was scored as absent in specimens lacking a median prefrontal.

Prefrontal Length 2 (RPFL2). Ratio of the length along the midline of the lateral prefrontal (Fig. 1: 4 to 6) divided by length of the midline suture of the nasals (Fig. 1: 1 to 2).

Frontal Length 2 (RFL2). Ratio of the length of the midline suture of frontals (Fig. 1: 8 to 9) divided by length of the midline suture of postparietals (Fig. 1: 15 to 17).

RESULTS AND DISCUSSION
ANALYSIS OF VARIATION AND
DELINEATION OF SPECIES

Southern Groups

An initial discriminant function analysis was performed with the 30 basic meristic and mensural scale characters (excluding the presence/absence of the parietal spot; Table 1) for all 129 locality samples from southern México (below 19°N) and Central America. The analysis revealed three nonoverlapping multivariate clusters (groups S, T, and F), that each contain multiple locality samples (Fig. 4). For these three groups, variation in individual characters among the samples is analyzed, the diagnosable units are identified, and species names are assigned. In addition to these three multilocality groups, the initial discriminant analysis identified three clusters (D, L, and R), which each contain a single locality sample. Previous work (Bezy and Camarillo, 1992, 1997) demonstrated that each of the three samples represents a morphologically discrete species (*L. dontomasi* Smith, 1942; *L. lowei* Bezy and Camarillo, 1997; and *L. radula* Smith,

Table 2. Extended.

RPBW	M	MC	RML2	RPFL2	RFL2
0.41–0.71 (0.62)	0	0	—	1.44–4.88 (2.53)	0.60–0.89 (0.77)
0.81–0.87 (0.84)	1	0–1 (0.50)	0.14–0.21 (0.18)	1.55–2.49 (2.02)	1.39–1.48 (1.44)
0.56	1	—	—	—	—
0.54	1	0	0.62	3.64	0.88
0.91–1.35 (1.09)	0	0	—	2.56–4.24 (3.45)	0.39–0.67 (0.50)
0.40–1.10 (0.68)	0–1 (0.47)	0–1 (0.08)	0.13–0.80	1.00–4.50 (2.45)	0.23–1.70 (0.79)
0.64–0.65 (0.64)	0	0	—	3.40–3.62 (3.51)	0.47–0.67 (0.57)
0.40–1.10 (0.65)	0–1 (0.33)	0	0.13–0.47 (0.31)	1.00–3.50 (2.33)	0.29–1.62 (0.75)
0.53–0.90 (0.74)	0–1 (0.20)	0–1 (0.20)	0.26–0.80 (0.53)	1.46–4.50 (2.43)	0.35–1.35 (0.86)
0.33–1.01 (0.63)	0–1 (0.99)	0–1 (0.36)	0.36–0.99 (0.56)	1.79–15.15 (3.55)	0.24–1.32 (0.57)
0.44–1.01 (0.73)	1	1	0.38–0.62 (0.50)	2.41–3.86 (3.17)	0.35–0.73 (0.56)
0.33–1.24 (0.62)	0–1 (0.99)	0–1 (0.37)	0.04–0.99 (0.56)	1.79–15.15 (3.59)	0.24–1.32 (0.58)
0.42–1.24 (0.65)	1	0–1 (0.95)	0.48–1.08 (0.74)	2.09–7.95 (3.58)	0.33–1.02 (0.62)
0.47–0.71 (0.57)	1	0	0.31–0.54 (0.44)	3.28–4.12 (3.61)	0.38–0.57 (0.46)

1942, respectively), and these analyses are not repeated here. However, all species of *Lepidophyma* recognized as valid are included in the summary and key.

GROUP S. The group contains 307 specimens from 33 localities on the Pacific slope from El Salvador to Michoacán (see Specimens Examined for a list of the names of Mexican states that are used in the text without reference to country). Members of the group are characterized by the absence in adults (over 75 mm SVL) of an externally visible parietal spot (PS; Table 1).

Discriminant function analysis of variation in the 30 characters among the samples of group S revealed that the specimens from Michoacán and Guerrero each constitute a discrete cluster (S1 and S2, respectively), with a third cluster (S3) composed of multivariately overlapping samples from Oaxaca to El Salvador (Fig. 5).

The Michoacán cluster (S1) contains 4 specimens from 2 localities. Univariate comparisons among samples in group S indicate that the specimens from Michoacán have discrete (nonoverlapping) differences in number of dorsals and gulars from all oth-

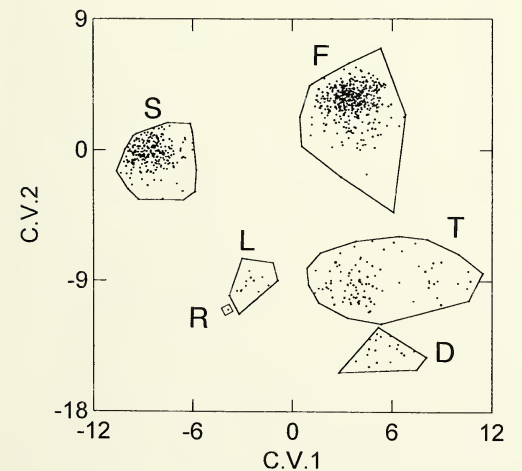


Figure 4 Plots of individual specimen scores on the first two canonical variates for 129 locality samples of *Lepidophyma* from southern México and Central America. Envelopes enclose the specimens for the six nonoverlapping groups present.

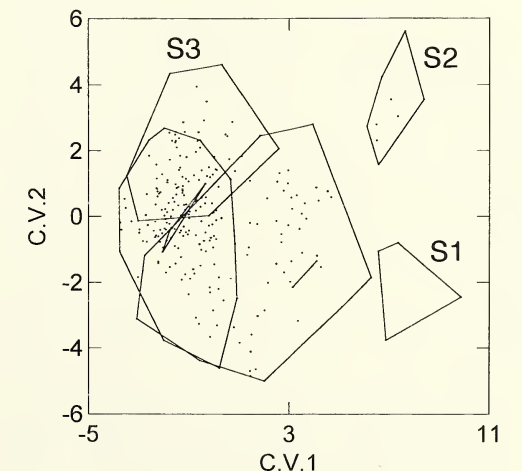


Figure 5 Plots of individual specimen scores on the first two canonical variates for locality samples of group S of *Lepidophyma* (from Fig. 4). Three nonoverlapping groups (S1, S2, and S3) are present.

Table 3. Variation in 12 scale characters among samples of group T of *Lepidophyma*. The observed limits of variation are followed by the mean (in parentheses).

	N	FPT	LTR	IWD2	PTMP	PVTL
<i>L. mayae</i>						
Guatemala	16	29–35 (32.3)	33–46 (0.83)	3–4 (3.9)	1–2 (1.9)	21–46 (34.5)
<i>L. pajapanense</i>						
Veracruz	22	30–36 (0.33)	36–43 (40.0)	3–4 (3.1)	6–10 (7.5)	39–51 (43.5)
<i>L. tuxtlae</i>						
Veracruz						
Los Tuxtlas	85	20–29 (24.5)	30–37 (34.0)	2–5 (3.6)	4–9 (5.5)	30–49 (39.2)
Jésus Carranza	1	25	34	3	5	41
Oaxaca						
Vista Hermosa	6	18–26 (23.5)	35–40 (36.5)	4–5 (4.2)	4–8 (5.7)	34–45 (39.3)
La Gloria	1	26	35	4	5	46
Matias Romero	1	23	—	3	5	—
Chiapas						
Ocote	4	25–26 (25.5)	31–33 (31.5)	3–4 (3.8)	4–6 (4.8)	40–46 (43.3)

er members of the group (Table 2). The cluster contains the holotype of *L. tarascae* Bezy, Webb, and Álvarez, 1982, and this name is assigned to these specimens.

The Guerrero cluster (S2) contains 17 specimens from 1 locality, and these have a higher average number of femoral pores than other members of group S (Table 2). However, the observed limits of variation for femoral pores in the Guerrero sample (S2) slightly overlap those of specimens from Oaxaca and Chiapas (S3), and thus clusters S2 and S3 are judged to be conspecific.

Comparisons among the samples of S2 and S3 reveal that 2 localities appear to share a scale feature that is nonoverlapping with other members of

the group. The two individuals from Cafetal El Pacífico (LACM 134844, UCM 48452) and one damaged specimen from the adjacent locality of Cafetal Alemania (AMNH 15977) in the Sierra Madre del Sur of Oaxaca differ in number of lateral tubercle rows from all other specimens of clusters S2 and S3 (Table 2). The 3 specimens include the holotype of *L. flavimaculatum lineri* Smith, 1973, and they are recognized as a distinct species, *L. lineri*.

Smith (1973) originally described this taxon as a subspecies of *L. flavimaculatum*, characterized by the following features (abbreviations in parentheses denote equivalent characters in Table 2): a minute median prefrontal (RML2), subtriangular lateral prefrontals (RPFL2), a large frontal (RFL2), and large lateral preanals (RPAW). The 2 specimens of *L. lineri* from the type locality appear to have average differences from other samples of clusters S2 and S3 in these 4 characters, but there is extensive overlap in the observed limits of variation (Table 2). As noted by Smith (1973) the diagnostic value of the presence of keeled ventrals in this taxon is questionable because the known specimens have a small snout–vent length and this feature is negatively correlated with body size (Fig. 6). Although the original diagnostic features used by Smith (1973) appear to be overlapping with other samples, the 2 specimens from the type locality (El Pacífico, Oaxaca) have a distinctly higher number of lateral tubercle rows, a feature shared with the specimen from the adjacent locality, Cafetal Alemania (Table 2). *Lepidophyma lineri* is here recognized as a separate species on the basis of its discrete difference in number of lateral tubercle rows from other members of group S, but this conclusion must be considered tentative because the taxon is represented by only 3 specimens.

Although significant differences exist among some of the other samples in S2 and S3, there is

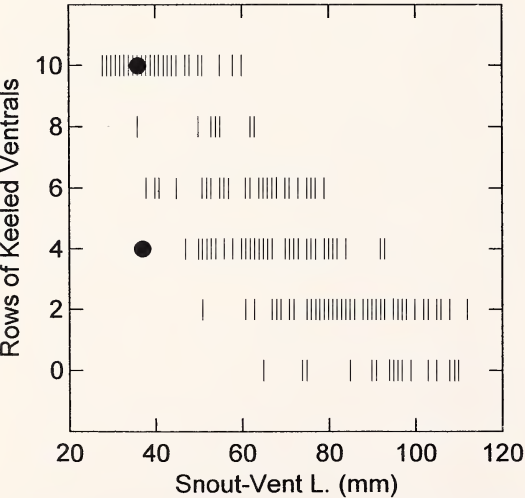


Figure 6 Number of longitudinal rows of ventral scales bearing keels plotted against snout–vent length for specimens of *Lepidophyma lineri* (filled circles) and *L. smithii* (vertical lines).

Table 3. Extended.

FTL	FTLD	DOR	DAPVR	MC	RML	RPAW
23–28 (25.1)	10–19 (14.8)	162–188 (174.8)	72–91 (79.7)	0–1 (0.81)	1.09–2.16 (2.49)	0.38–0.77 (0.50)
26–30 (28.5)	10–18 (14.2)	152–177 (165.1)	59–82 (70.0)	0–1 (0.32)	1.00–2.81 (1.73)	0.38–0.69 (0.54)
23–29 (26.0)	13–21 (16.6)	158–190 (173.5)	69–98 (80.2)	0–1 (0.89)	0.49–3.15 (1.32)	0.56–1.12 (0.83)
26	15	169	76	0	1.24	0.83
22–26 (23.3)	12–15 (13.8)	150–171 (159.2)	71–84 (76.3)	0–1 (0.67)	0.54–2.20 (1.34)	0.70–0.87 (0.80)
—	—	163	77	0	0.98	0.73
25	14	—	—	0	0	0.74
26–27 (26.5)	14–16 (14.8)	165–177 (171.0)	73–80 (77.8)	0–1 (0.25)	0.00–1.66 (0.91)	0.59–0.68 (0.63)

overlap in the observed limits of variation for all scale characters examined and the remaining samples in these clusters are considered to represent a single species. Cluster S3 includes the holotypes of *L. smithii* Bocourt, 1876; *Akleistops guatemalensis* Muller, 1877; and *L. smithii tehuanae* Smith, 1942. The oldest available name, *L. smithii*, is assigned to the remaining members of clusters S2 and S3.

Smith (1942, 1973) distinguished *L. flavimaculatum tehuanae* from *L. flavimaculatum smithii* by its lack of a median prefrontal. The presence (M) and size (RML2) of the median prefrontal and the presence of a contact between the median prefrontal and the frontal (MC) appear to vary geographically (Table 2). A median prefrontal is present in 33% of the specimens from the vicinity of Tehuantepec, Oaxaca, which encompasses the type locality

of *L. f. tehuanae*. No discrete differences between *L. f. tehuanae* and *L. smithii* are apparent in any of the scale characters examined in this study (Table 2) and the two are considered conspecific. The relationship of *L. smithii* to *L. flavimaculatum* is discussed under group F, below.

On the basis of the above comparisons it is concluded that group S contains 3 morphologically discrete species: *L. tarascae* (Michoacán), *L. lineri* (two localities in the Sierra Madre del Sur, Oaxaca), and *L. smithii* (Pacific slope from Guerrero to El Salvador).

GROUP T. The group contains 136 specimens from 13 localities from Veracruz and Oaxaca to Guatemala. Discriminant function analysis of variation in the 30 characters indicates that the samples form three discrete clusters (T1, T2, and T3; Fig. 7).

Cluster T1 is composed of 16 specimens from 4 localities in Guatemala. Univariate comparisons identify no discrete differences among the 4 locality samples. Cluster T1 differs from all specimens of clusters T2 and T3 in pretympenics and from *L. smithii*, *L. lineri*, and *L. tarascae* in lateral tubercle rows (Table 1). The cluster contains one holotype, that of *L. mayae* Bezy, 1973, and this name is applied to the species.

Cluster T2 contains 22 specimens from 3 regions in Veracruz. Univariate comparisons identify no discrete differences among the samples from these regions. The specimens in cluster T2 differ from all individuals of cluster T3 in femoral pores and fourth toe lamellae and from *L. smithii*, *L. lineri*, and *L. tarascae* in lateral tubercle rows and large paravertebrals (Table 1). The cluster contains the holotype of *L. pajapanense* Werler, 1957, and this name is applied to the species.

Cluster T3 includes 98 specimens from 6 localities in Veracruz, Oaxaca, and Chiapas. Univariate comparisons among the six samples do not reveal

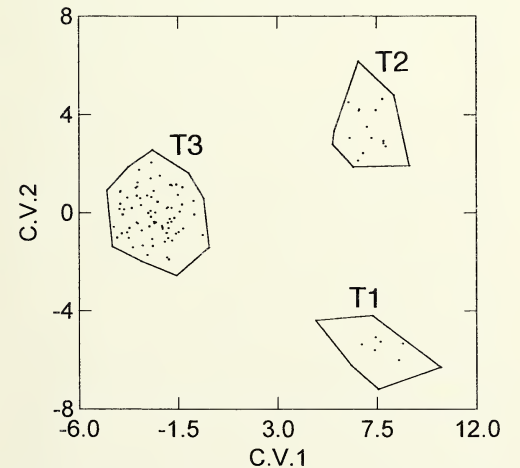


Figure 7 Plots of individual specimen scores on the first two canonical variates for locality samples of group T of *Lepidophyma* (from Fig. 4). Three nonoverlapping groups (T1, T2, and T3) are present.

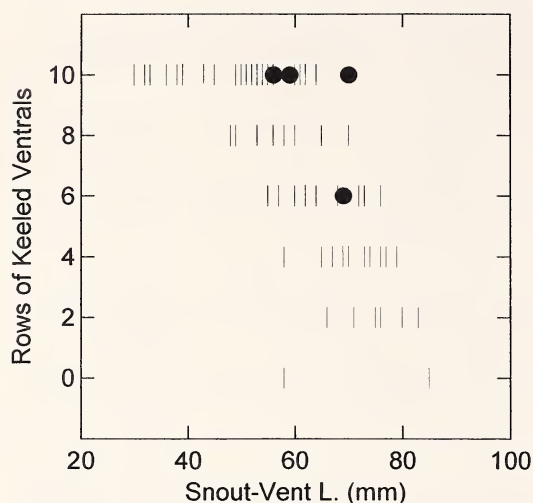


Figure 8 Number of longitudinal rows of ventral scales bearing keels plotted against snout-vent length for specimens of *Lepidophyma tuxtlae* from the Ocote region of Chiapas (filled circles) and the Tuxtla region of Veracruz (vertical lines).

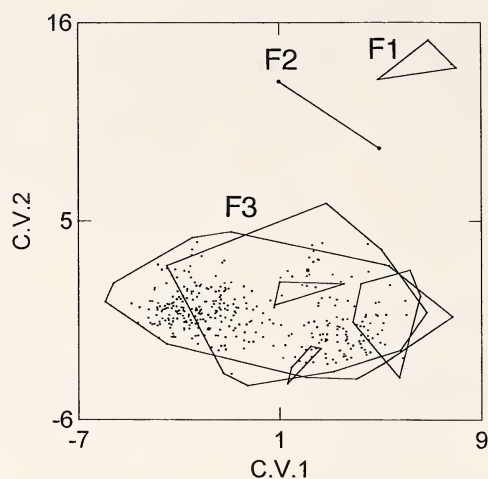


Figure 9 Plots of individual specimen scores on the first two canonical variates for locality samples of group F of *Lepidophyma* (from Fig. 4). Three nonoverlapping groups (F1, F2, and F3) are present.

any discrete differences. The specimens in cluster T3 differ from *L. smithii*, *L. lineri*, and *L. tarascae* in lateral tubercle rows and large paravertebrals. The cluster includes the holotypes of *L. tuxtlae* Werler and Shannon, 1957; *L. sawini* Smith, 1973; and *L. alvarezii* Smith, 1973. The oldest available name, *L. tuxtlae*, is assigned to the members of T3.

Smith (1973) described *L. alvarezii* based on a specimen from the Ocote region of Chiapas. It was distinguished from *L. tuxtlae* by having keeled ventrals, smaller lateral preanals, and a smaller median prefrontal. The 4 specimens (of group T3) examined from the Ocote region have slight average differences from the sample of *L. tuxtlae* from the Tuxtla region in relative sizes of the median prefrontal and lateral preanals and in number of femoral pores, lateral tubercle rows, pretympansics, large paravertebrals, and dorsals along the paravertebral row, but there is overlap in the ranges of variation for all scale characters examined (Table 3). The number of longitudinal rows of ventrals bearing keels is negatively correlated with snout-vent length and only one of the 4 Ocote specimens is outside of the range of variation found in the *L. tuxtlae* from the Tuxtla region (Fig. 8). *Lepidophyma alvarezii* is considered conspecific with *L. tuxtlae*.

A second species, *L. sawini*, was described by Smith based on a specimen from near Vista Hermosa, Oaxaca. It was distinguished from *L. tuxtlae* by having relatively large keeled scales bordering the paravertebrals medially. Compared to *L. tuxtlae* from the Tuxtla region, the 6 specimens now available from the Vista Hermosa region have slightly larger (fewer) scales bordering the para-

vertebrals medially (DAPVR; Table 3), but there is extensive overlap in the observed limits of variation. The Vista Hermosa specimens have virtually the same numbers of femoral pores as *L. tuxtlae* from the Tuxtla region and the observed limits of variation do not overlap those of *L. pajapanense* (Table 3). The Vista Hermosa specimens resemble *L. tuxtlae* (rather than *L. pajapanense*) from the Tuxtla region in color pattern (Figs. 23, 30). Although there are slight average differences between the Vista Hermosa sample and *L. tuxtlae* from the Tuxtla region (Table 3) in lateral tubercle rows, dorsal caudal interwhorls, fourth toe lamellae, divided fourth toe lamellae, dorsals, and dorsals along paravertebral row, there is overlap in all characters examined and *L. sawini* is considered conspecific with *L. tuxtlae*.

Three species are recognized as valid in group T: *L. mayae* (Guatemala), *L. pajapanense* (Veracruz), and *L. tuxtlae* (Veracruz, Oaxaca, and Chiapas).

GROUP F. The group contains 507 specimens from 80 localities in Veracruz and Oaxaca to Panamá. Discriminant function analysis with the 30 characters indicates that the samples form three clusters: F1, F2, and F3 (Fig. 9).

Cluster F1 contains 4 specimens from 1 locality in Chiapas. The specimens differ from members of clusters F2 and F3, as well as from all other *Lepidophyma*, in having a greater number of fourth toe lamellae (Table 1). All 4 specimens have 12 longitudinal rows of ventrals at midbody (contra Álvarez and Valentín, 1988), a condition that is rare within *Lepidophyma*, but present in one or more individuals of 6 other species of the genus (Table 1). The cluster contains the holotype of *L. chicoas-*

ense Álvarez and Valentín, 1988, and this name is applied to the species.

Cluster F2 contains 2 specimens from 1 locality (Río de La Venta) in Chiapas. Although the specimens share some distinctive features, there are notable differences between them in several scale characters (Fig. 9) and the 2 are discussed separately. One of the specimens, the holotype of *L. lipetzi* Smith and Álvarez del Toro, 1977 (UCM 51425), has a higher number of large paravertebral tubercles than do all members of cluster F3. In addition, it differs in having a higher number of dorsal scales and in having a pale color pattern from all F3 specimens from Chiapas, including those from the sympatric (Río de La Venta) and nearby (Selva Ocote) localities. It resembles the 4 specimens of *L. chicaoense* in having 12 longitudinal rows of ventrals and a pale color pattern, but differs in number of fourth toe lamellae.

The second F2 specimen (ENEPI 3792) from Río de La Venta resembles the holotype of *L. lipetzi* in number of lateral tubercle rows and dorsals and in having a pale color pattern, clearly differing from sympatric (La Venta) and nearby (Ocote) specimens of group F3 in these characters. However, it differs from the holotype in having 11 (vs 12) longitudinal ventral rows, the sixth row from the midline being clearly larger than the adjacent tubercles on only one side of the body. It also differs from the holotype in number of large paravertebral tubercles, resembling F3 specimens in this feature. It is tentatively grouped with the holotype in *L. lipetzi*. The 2 specimens thus assigned to *L. lipetzi* differ from *L. chicaoense* in fourth toe lamellae; from *L. smithii*, *L. lineri*, *L. tarascae*, and *L. tuxtlae* in femoral pores; and from *L. mayae* and *L. pajapanense* in gulars (Table 1). They differ in color pattern from all members of group F3 and in number of dorsal scales from sympatric (La Venta) and nearby (Ocote) localities for that group.

Variation among Central American locality samples of cluster F3 was examined in detail previously (Bezy, 1989) and resulted in the recognition of *L. reticulatum* Taylor, 1955 (Pacific slope of Costa Rica) as distinct from *L. flavimaculatum* Duméril, 1851 (Atlantic slope from México to Panamá); these analyses are not repeated here. The discriminant function analyses indicate that all samples of *L. flavimaculatum* from southern México (except those from Chiapas) cluster with samples from northern Central America (Guatemala to Honduras). The samples from Chiapas broadly overlap both the southern (Nicaragua to Panamá) and northern Central American clusters. No discrete univariate differences are apparent among the samples of *L. flavimaculatum* from southern México.

Lepidophyma flavimaculatum has discrete differences in scalation (Table 1) from *L. lineri* and *L. tarascae* (femoral pores), *L. chicaoense* (fourth toe lamellae), and *L. tuxtlae* and *L. pajapanense* (large paravertebral tubercles). It differs from sympatric *L. mayae* in lateral tubercle rows and pretymp-

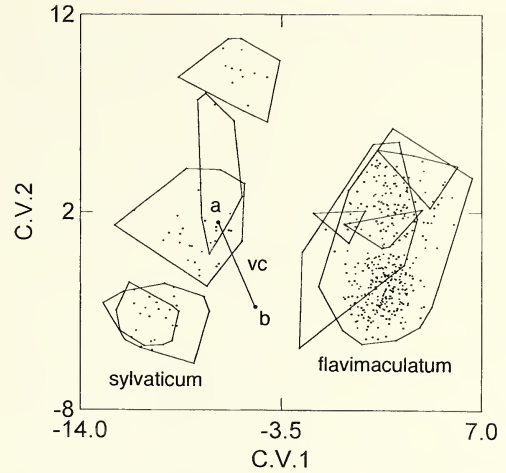


Figure 10 Plots of individual specimen scores on the first two canonical variates for locality samples of *Lepidophyma sylvaticum* and *L. flavimaculatum*. Of the 2 specimens of *L. sylvaticum* from Veracruz (VC), the more southern one (a) is placed within *L. sylvaticum*, whereas the more northern one (b) is placed intermediate between the two species.

ics, and from sympatric (Chiapas) *L. lipetzi* in number of dorsals.

Lepidophyma flavimaculatum and *L. smithii* comprise multivariately discrete clusters (groups F and S in Fig. 4), including the specimens from where their ranges are in close proximity in Oaxaca. Throughout the extensive ranges of the 2 species they differ in lateral tubercle rows. In addition, *L. flavimaculatum* has an externally visible pale parietal spot that is absent in adult *L. smithii* (SVL greater than 75 mm). The 2 also differ in karyotype (Bezy, 1972) and are recognized as discrete species.

Four species are recognized as valid in group F: *L. chicaoense* (Chiapas), *L. lipetzi* (Chiapas), *L. reticulatum* (Costa Rica), and *L. flavimaculatum* (Veracruz and Oaxaca to Panamá).

Comparisons with Species in Northeastern México

Bezy (1984) recognized 4 species of *Lepidophyma* as valid in northeastern México: *L. gaigeae* Mosauer, 1936; *L. micropholis* Walker, 1955; *L. ocellator* Smith, 1942; and *L. sylvaticum* Taylor, 1939. *Lepidophyma micropholis* differs in number of dorsals (Table 1) from all southern species delineated above. *Lepidophyma gaigeae* also differs in dorsals from all southern species except *L. radula*, from which it differs in femoral pores. *Lepidophyma ocellator* differs in gulars from all southern species except *L. smithii*, from which it differs in having a parietal spot in adults and a different karyotype.

Lepidophyma sylvaticum has discrete differences (Table 1) from *L. tarascae* and *L. lineri* (femoral pores), *L. tuxtlae* (dorsals separating paravertebral

tubercles), *L. pajapanense* (pretympanics), *L. chicoasense* (fourth toe lamellae), *L. smithii* (presence of a pale parietal spot in adults), *L. lipetzi* (height of second postorbital infralabial), and *L. mayae* (median prefrontal width).

Lepidophyma sylvaticum and *L. flavimaculatum* form discrete multivariate clusters (Fig. 10). Where their ranges are in close proximity in Veracruz, the 6 specimens of *L. flavimaculatum* and the southernmost specimen of *L. sylvaticum* (Fig. 10, point a; MZFC 1722 from Alvarado) are placed well within their respective species clusters. However, the more northern Veracruz specimen of *L. sylvaticum* (Fig. 10, point b; KU 26909 from Tlapacoyam) is placed somewhat intermediate between the 2 species clusters. Nevertheless, the 2 *L. sylvaticum* and 6 *L. flavimaculatum* from Veracruz are non-overlapping in 5 scale characters (femoral pores, lateral tubercle rows, caudal interwhorls, pretympanics, gulars contacting the first infralabials, and height of the second postorbital supralabial). For the 545 specimens examined from throughout the ranges, the 2 species generally differ in number of pretympanics and in the relative height of the second postorbital supralabial. All but one *L. flavimaculatum* (UCM 49278 from Chiapas) have 4 or more pretympanics and all but 2 *L. sylvaticum* (AMNH 107273, UMMZ 101374, both from Tamaulipas) have 3 or fewer pretympanics. For the relative height of the second postorbital supralabial, all specimens of *L. sylvaticum* have a RSLH of 0.84 or greater, and all but 3 specimens of *L. flavimaculatum* (UMMZ 113777 from Tobasco, MVZ 159933 from Guatemala, AMNH 107589 from Panamá) have a RSLH of less than 0.84. No specimens overlap in both characters. The 2 also have consistent differences in the number and morphology of chromosomes (Bezy, 1984) and are considered to represent discrete species.

SUMMARY OF THE EXTANT SPECIES OF THE GENUS *LEPIDOPHYMA*

Lepidophyma A. Duméril

Lepidophyma A. Duméril, in Duméril and Duméril, 1851:137. Type species: *Lepidophyma flavimaculatus* A. Duméril.

Poriodogaster Smith in Gray, 1863:154, Plate XXI. Type species: *Poriodogaster grayii* Smith.

Akleistops Muller, 1877:390, Tafel I, II. Type species, *Akleistops guatemalensis* Muller.

Gaigeia Smith, 1939:24. Type species: *Lepidophyma gaigeae* Mosauer.

DIAGNOSTIC CHARACTERS. The living members of the genus *Lepidophyma* differ from *Cricosaura typica* (condition in parentheses) in having 1 frontonasal (2), 2 frontals (1), and 2 parietals (none); and from living members of the genus *Xantusia* (condition in parentheses) in having a round pupil (vertically elliptical); in having the nostrils placed in the suture between the nasal and post-

nasal (in the suture between the nasal, postnasal, and rostral); and no postmentals (postmentals distinct from infralabials; Savage, 1963; R.L. Bezy and J.L. Camarillo, personal observations).

CONTENT. A total of 17 extant species of *Lepidophyma* are recognized as a result of this study: *L. chicoasense*, *L. dontomasi*, *L. flavimaculatum*, *L. gaigeae*, *L. lineri*, *L. lipetzi*, *L. lowei*, *L. mayae*, *L. micropholis*, *L. occulor*, *L. pajapanense*, *L. radula*, *L. reticulatum*, *L. smithii*, *L. sylvaticum*, *L. tarascae*, and *L. tuxtlae*. The validity of *L. arizeloglyphum* (Langebartel, 1953) and other fossil taxa (Estes, 1983) not included in this study requires additional investigation focusing on osteology.

KARYOTYPES. The diploid chromosome numbers of species in the genus range from 32 to 38; numbers of macrochromosomes, from 16 to 18; and numbers of microchromosomes, from 16 to 20 (Bezy, 1972; Bezy and Camarillo, 1992, 1997). The karyotypes of members of *Lepidophyma* differ from those of members of *Xantusia* (Bezy, 1972; Bezy and Flores Vilella, 1999) in having lower diploid numbers (32–38 vs 40) and fewer microchromosomes (16–20 vs 22); and from that of *Cricosaura typica* (Hass and Hedges, 1992) in having higher diploid numbers (32–38 vs 24), and higher numbers of macrochromosomes (16–18 vs 12) and microchromosomes (16–20 vs 12).

SIZE. The maximum snout–vent length of the 12 species for which 10 or more individuals were examined ranges from 56 mm (*L. dontomasi*, N = 23) to 127 mm (*L. flavimaculatum*, N = 432).

DISTRIBUTION, HABITAT, AND NATURAL HISTORY. Extant species of *Lepidophyma* are found from Nuevo León and Michoacán, México, to Panamá, (Figs. 11, 12), excluding most of the Yucatán peninsula (where the extinct *L. arizeloglyphum* was found). The greatest species diversity occurs in the region of Oaxaca and Chiapas, México (10 species), and in the ranges and valleys associated with the northern Sierra Madre Oriental in Querétaro and San Luis Potosí, México (4 species). Members of the genus occur in a broad range of vegetation types from semiarid thorn scrub to tropical wet forest, cloud forest, and pine and pine-oak woodland. The lizards are found under a variety of cover, including rocks, logs, tree stumps, bark, and forest litter; in rock crevices, caves, culverts, and walls; and within human dwellings. Both diurnal and nocturnal activity have been observed, and diet includes fruit and arthropods (Campbell, 1998; Mautz and López-Forment, 1978). The 5 species for which reproductive information is available are viviparous.

REMARKS. *Lepidophyma dontomasi*, *L. gaigeae*, *L. lowei*, and *L. radula* form a distinct phenetic cluster within the genus characterized by small body size, absence of microtubercles on the scale surfaces (Bezy and Peterson, 1988); absence (or small size) of tubercular scales on the body (except *L. radula*); poorly differentiated caudal whorls and interwhorls; and relatively large (and thus few)

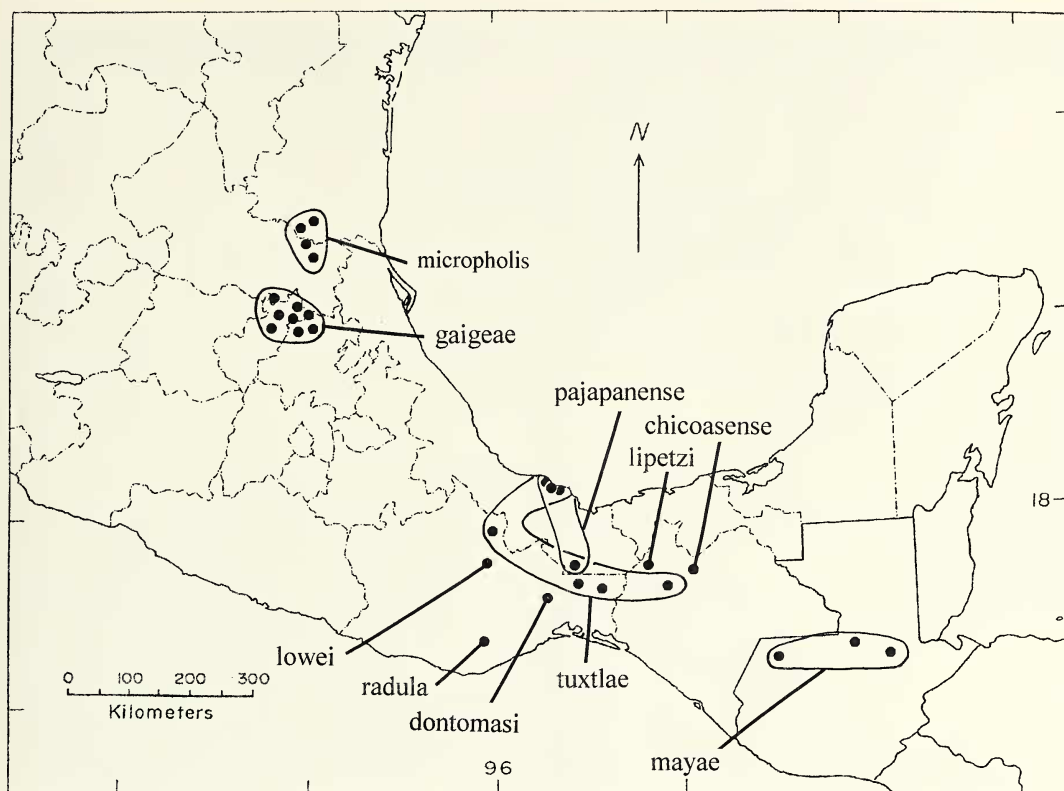


Figure 11 Geographic distribution of 10 species of *Lepidophyma*.

dorsal, ventral, and gular scales (Bezy and Camarillo, 1992, 1997). Whether the 4 species comprise a clade (*Gaigeia*; Smith, 1939, 1973) or a grade is being addressed by phylogenetic analyses of DNA sequences combined with morphology (R.L. Bezy and collaborators, unpublished).

ETYMOLOGY. The name *Lepidophyma* (Greek: *lepidos*, scale; *phyma*, enlarged or swollen object) is neuter (Smith, 1973) and refers to the presence of enlarged tubercular scales.

COMMON NAMES. Tropical night lizards; lagartijas nocturnas tropicales; escorpiones nocturnos.

Lepidophyma chicoasense Álvarez
and Valentín
Group F1; Figure 13

Lepidophyma chicoasensis Álvarez and Valentín, 1988:125, Fig. 1. Holotype: IPN 11132; type locality, "16.3 Km N, 1.6 Km E de Tuxtla Gutiérrez, 600 m., Chiapas, México."

DIAGNOSTIC CHARACTERS. The species differs from all other *Lepidophyma* in having 35 or more fourth toe lamellae. It differs from all except *L. smithii*, *L. flavimaculatum*, *L. micropholis*, and *L. sylvaticum* in having 53 or more gulars; from *L.*

gaigeae, *L. dontomasi*, *L. lowei*, *L. radula*, *L. tarascae*, and *L. pajapanense* in having 177 or more dorsals; and from *L. reticulatum*, *L. micropholis*, and *L. occulor* in having 192 or fewer dorsals (Table 1).

KARYOTYPE. Unknown.

SIZE. The maximum snout-vent length for the 4 specimens examined is 78 mm.

SEX RATIO. Of the 3 specimens sexed, 2 (67%) are males.

DISTRIBUTION, HABITAT, AND NATURAL HISTORY. The species is known only from the type locality located in the Cañón Sumidero (Fig. 11).

REMARKS. *Lepidophyma chicoasense* resembles *L. lipetzi* in color pattern and in many features of scalation, including the presence of 12 longitudinal rows of ventrals at midbody (contra Álvarez and Valentín, 1988). However, it has a higher number of fourth toe lamellae than all other members of the genus, including *L. lipetzi*, *L. flavimaculatum*, and *L. tuxtlae*, which occur in the region.

ETYMOLOGY. The name *chicoasense* is an adjective and refers to La Presa de Chicoasén, Chiapas, located in the region of the type locality. The original name is emended in this paper to modify the neuter generic name.

COMMON NAMES. Sumidero Tropical Night Lizard; Lagartija Nocturna del Sumidero.

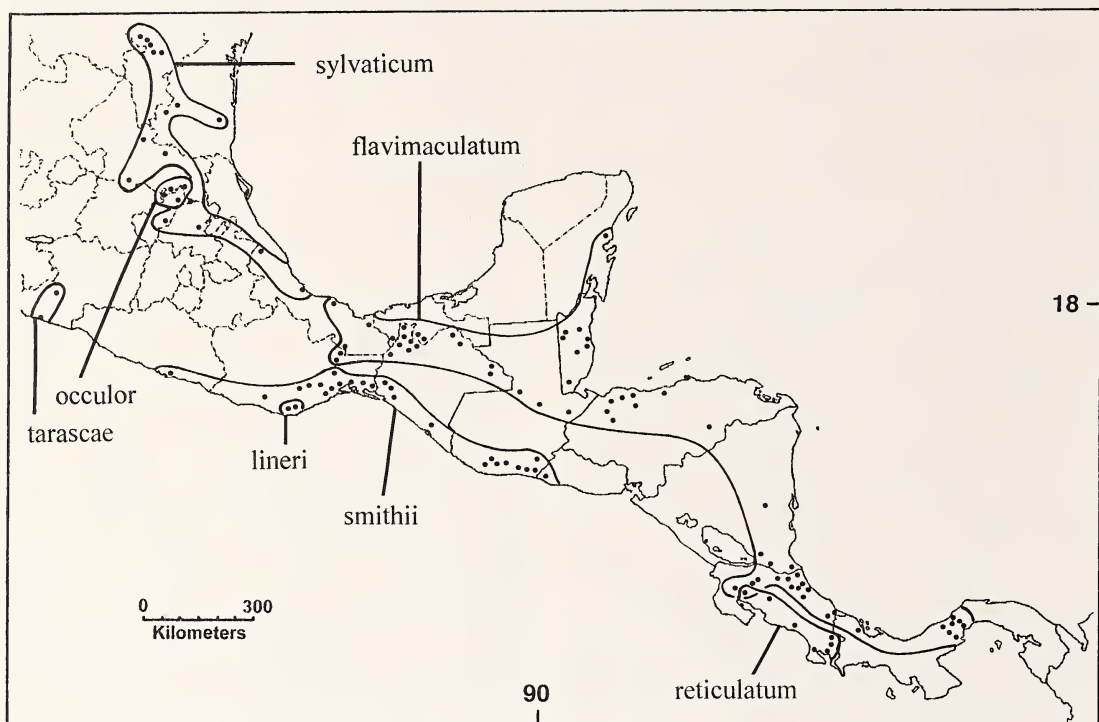


Figure 12 Geographic distribution of seven species of *Lepidophyma*.

Lepidophyma dontomasi (Smith)

Group D; Figure 14

Gaigeia dontomasi Smith, 1942:374. Holotype: USNM 111473; type locality, "Lachiguiri, Oaxaca, at 7,100 feet."

Lepidophyma dontomasi: Savage, 1963:35.

DIAGNOSTIC CHARACTERS. The species differs from all other *Lepidophyma* except *L. lowei* and *L. radula* in having enlarged caudal whorls that are separated dorsally by 2 rows of interwhorls, only one of which is complete ventrally; from all except *L. gaigeae*, *L. radula*, and *L. tarascae* in having 149 or fewer dorsals; from *L. gaigeae* in having 21 or fewer femoral pores; from *L. tarascae* in having 35 or fewer gulars (Table 1); and from *L. radula* in lacking vertical rows of distinctly enlarged tubercles on the side of the body.

KARYOTYPE. *Lepidophyma dontomasi* has a diploid chromosome number of 32 with 16 macrochromosomes and 16 microchromosomes (Bezy and Camarillo, 1992). The macrochromosomes are very similar to those of *L. smithii*. The species has the lowest number of total chromosomes and of microchromosomes in the genus.

SIZE. The maximum snout-vent length for the 29 specimens examined is 56 mm, smaller than any other member of the genus except *L. radula* (known only from the holotype).

SEX RATIO. Of the 22 specimens sexed, 9 (41%) are males.

DISTRIBUTION, HABITAT, AND NATURAL HISTORY. The species is known only from the type locality on Cerro Lachiguiri, Oaxaca (Fig. 11), where it has been found under logs in pine forest (Smith, 1942) and in rock crevices and under rocks and dead *Agave* and *Nolina* in oak savanna (Bezy and Camarillo, 1992).

REMARKS. Additional field work is needed to determine if the species occurs elsewhere in the Sierra de los Mijes.

ETYMOLOGY. The name *dontomasi* is a noun in the genitive singular case and honors Thomas (Don Tomas) Baillie MacDougall (1896–1973), a naturalist who collected plants and animals (including the holotype of *L. dontomasi*) from remote areas in México, particularly the Tehuantepec region (Smith, 1974).

COMMON NAMES. MacDougall's Tropical Night Lizard; Lagartija Nocturna de MacDougall.

Lepidophyma flavimaculatum complex

Group F3; Figure 15

Lepidophyma flavimaculatus A. Duméril in Duméril and Duméril, 1851:138. Holotype: MNHN 782; type locality, "Province du Petén (America centrale)" (restricted to Río de la Pasión, Guatemala, by Smith and Taylor, 1950).

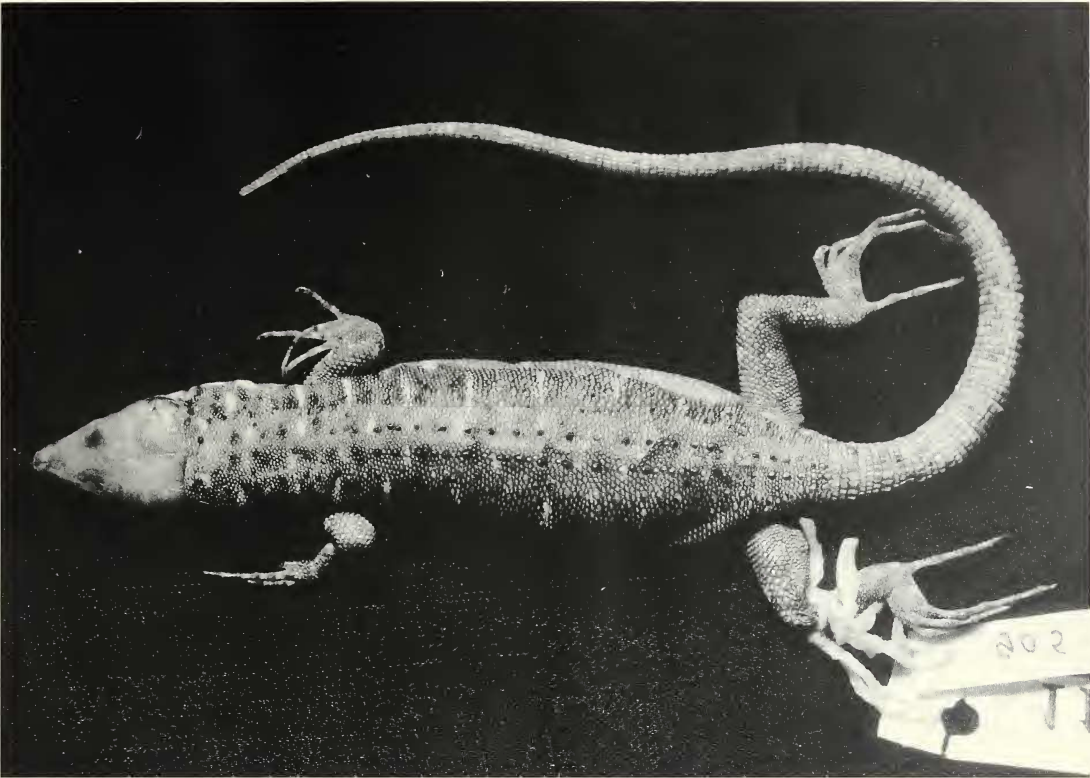


Figure 13 The holotype of *Lepidophyma chicoasense* (IPN 11132; snout–vent length, 78 mm).

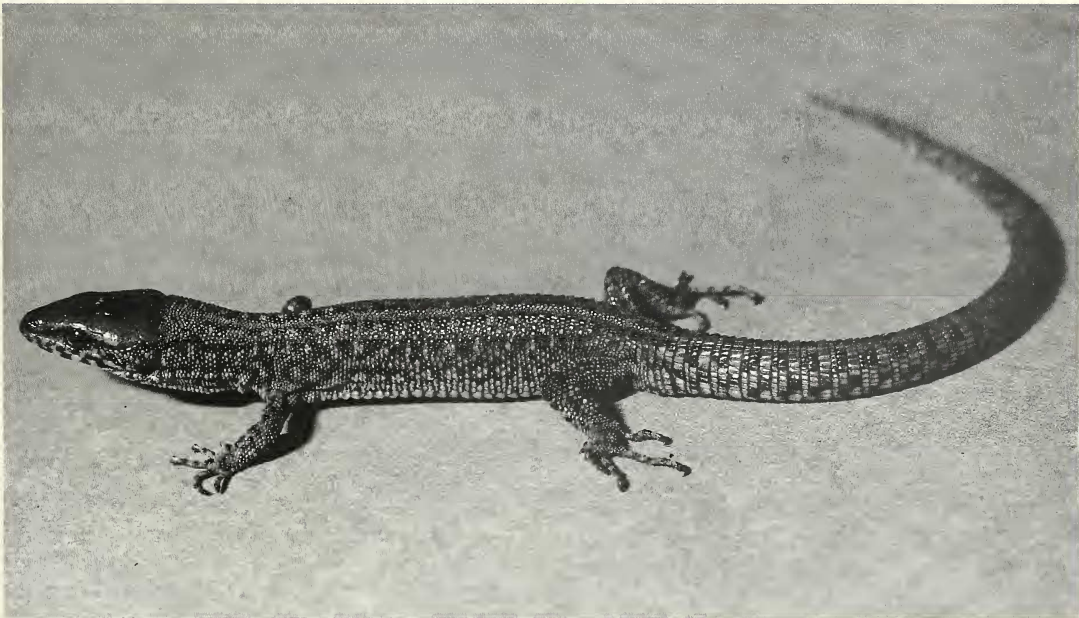


Figure 14 Living individual of *Lepidophyma dontomasi* (ENEPI 3016; snout–vent length, 50 mm).

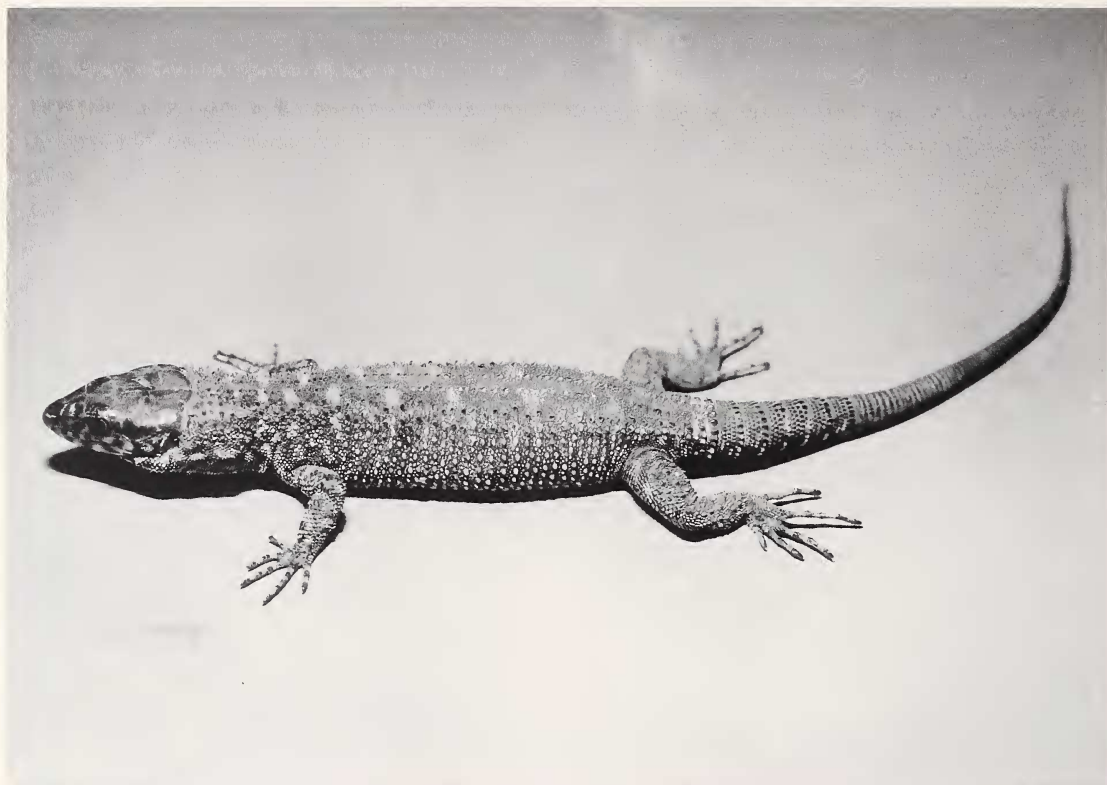


Figure 15 Living individual of *Lepidophyma flavimaculatum* (ENEPI 3793; snout–vent length, 107 mm).

Lepidophyma flavimaculatum: A.H.A. Duméril, 1852, Plate 17.

Poriodogaster grayii Smith in Gray, 1863:154, Plate XXI. Holotype: BMNH 1946.8.30.44; type locality, unknown (originally conjectured to be “Lower California” and subsequently thought by Peters, 1874, to be Panamá).

Lepidophyma flavomaculatum obscurum Barbour, 1924:10. Holotype: MCZ 17747; type locality, “Río Chilibrillo, Panamá.”

Lepidophyma flavomaculatum flavomaculatum: Smith, 1942:379.

Lepidophyma anomalum Taylor, 1955:554, Fig. 14. Holotype: KU 34207; type locality, “Los Diamantes, Guápiles, Limón Province, Costa Rica.”

Lepidophyma ophiophthalmum Taylor, 1955:558, Fig. 15. Holotype: KU 36250; type locality, “5 km. NNE Tilarán, Guanacaste, Costa Rica.”

DIAGNOSTIC CHARACTERS. The species differs from *L. dontomasi*, *L. radula*, *L. tarascae*, *L. lineri*, and *L. occulor* in having 25 or more femoral pores; from *L. dontomasi*, *L. gaigeae*, *L. radula*, and *L. tarascae*, in having 170 or more dorsals; from *L. dontomasi*, *L. lowei*, and *L. radula* in having 40 or more gulars; from *L. pajapanense* and *L. tuxtlae* in having 27 or fewer large paravertebral tubercles; from *L. smithii* in having 23 or more lat-

eral tubercle rows; from *L. micropholis* in having 225 or fewer dorsals; from *L. chicoasense* in having 31 or fewer fourth toe lamellae; from *L. lipetzi* in having 180 or more dorsals (99.3% of all *L. flavimaculatum*, 100% of Chiapas specimens) and a darker color pattern (Fig. 15); from *L. reticulatum* in lacking a boldly reticulated color pattern on the gular surface; from *L. mayae* in having 33 or fewer lateral tubercle rows (99.6% of all *L. flavimaculatum*, 100% of Guatemala specimens) and 3 or more pretympanics (99.8% of all *L. flavimaculatum*, 100% of Guatemala specimens); from *L. sylvaticum* in having 4 or more pretympanics (99.3% of all *L. flavimaculatum*) and a lower second post-orbital supralabial (0.83 or less; 99.3% of all *L. flavimaculatum*: Table 1); and from *L. reticulatum* in lacking a bold reticulations on the gular surface.

KARYOTYPE. *Lepidophyma flavimaculatum* has a diploid chromosome number of 38 with 18 macrochromosomes and 20 microchromosomes (Bezy, 1972). One individual from an all-female population appeared to be a diploid–triploid mosaic. The karyotype is identical to that of *L. pajapanense*, *L. tuxtlae*, and *L. reticulatum*. It differs from that of *L. sylvaticum* in having 18 rather than 16 microchromosomes.

SIZE. The maximum snout–vent length for the 432 specimens examined is 127 mm.

SEX RATIO. Of the 308 specimens sexed, 60 (19%) are males. No males were present in samples from Panamá and most populations in Costa Rica.

DISTRIBUTION, HABITAT, AND NATURAL HISTORY. The species is found primarily on the Atlantic versant from Veracruz and Oaxaca to Panamá, but absent from the outer Yucatán Peninsula (Fig. 12). It occurs in sympatry with *L. pajapanense* in Veracruz; with *L. tuxtlae* in Veracruz, Oaxaca, and Chiapas; with *L. lipetzi* in Chiapas; with *L. mayae* in Guatemala; and with *L. reticulatum* in Costa Rica. The species occurs at low and moderate elevations in tropical moist forest, tropical dry forest, and subtropical wet forest, where it is found in rotting logs and tree stumps; in forest litter; under bark; under rocks; and in rock crevices, caves, and ruins (Álvarez del Toro, 1982; Burt, 1935; Campbell, 1998; Duellman, 1963; Henderson and Hoeyers, 1975; Lee, 1996; Meyer and Wilson, 1973; Scott, 1976; Slevin, 1942; Stuart, 1948; Telford and Campbell, 1970; R.L. Bezy and colleagues, personal observations). It is reported to consume termites, ants, crickets, spiders, scorpions, centipedes, and millipedes, and to be preyed upon by the colubrid snakes *Dryadophis melanolomus* Cope, 1868, and *Drymarchon corais* Boie, 1827 (Campbell, 1998; Lieberman, 1986). In Chiapas, five to eight young are born in June and July (Álvarez del Toro, 1982), and in Panamá, a female gave birth in June to five neonates, all females (Telford and Campbell, 1970).

REMARKS. *Lepidophyma flavimaculatum* is unusually variable in scalation because of geographical variation among its widely scattered localities. It is most similar to *L. mayae*, *L. lipetzi*, and *L. sylvaticum*. In areas where it occurs with *L. mayae* and *L. lipetzi*, individual scale characters segregate all specimens, indicating reproductive isolation. Univariante scale characters separate 99% of the specimens of *L. flavimaculatum* from *L. sylvaticum*, and the 2 species differ in karyotype for all localities examined (*L. flavimaculatum* from Chiapas to Panamá and *L. sylvaticum* from Nuevo León to Hidalgo).

The term complex is used for the aggregation of *Lepidophyma flavimaculatum* populations to denote that it may contain more than 1 species. The populations in Panamá and most of Costa Rica lack males but do not appear to differ significantly in allozymes, karyotype, scalation, or color pattern from the populations to the northwest that contain males (Bezy, 1972, 1989; Bezy and Sites, 1987).

ETYMOLOGY. The name *flavimaculatum* (Latin: *flavus*, yellow; *maculatum*, spotted) is an adjective and refers to the dorsal color pattern. The original name was justifiably emended by A.H.A. Duméril (1852) to modify the neuter generic name.

COMMON NAMES. Yellow-spotted Tropical Night Lizard; Lepidofima; Escorpión Nocturno Puntos Amarillos; Reina de Culebra; Perrozompo atlántico.

Lepidophyma gaigeae Mosauer

Group G; Figure 16

Lepidophyma gaigeae Mosauer, 1936:3, Plate II. Holotype: MCZ 42145 (Mosauer Mexican Collection 971); type locality, "Durango, State of Hidalgo, México."

Gaigeia gaigeae: Smith, 1939:24.

DIAGNOSTIC CHARACTERS. The species differs from all other *Lepidophyma* except *L. tarascae* in having enlarged caudal whorls that are separated dorsally by 2 rows of interwhorls both of which are complete ventrally; from all except *L. dontomasi*, *L. radula*, *L. tarascae*, *L. tuxtlae*, and *L. sylvaticum* in having 151 or fewer dorsals; from *L. dontomasi*, *L. radula*, and *L. tarascae* in having 28 or more femoral pores; from *L. tuxtlae* in lacking paravertebral rows composed of a continuous string of subequal tubercles; and from *L. sylvaticum* in lacking distinctly enlarged tubercles on the side of the body (Table 1).

KARYOTYPE. *Lepidophyma gaigeae* has a diploid chromosome number of 38 with 18 macrochromosomes and 20 microchromosomes (Bezy, 1972). The karyotype is similar to that of *L. flavimaculatum*, *L. tuxtlae*, and *L. pajapanense*, but differs in centromere position for 2 pairs of chromosomes.

SIZE. The maximum snout-vent length for the 177 specimens examined is 66 mm.

SEX RATIO. Of the 147 specimens sexed, 55 (37%) are males.

DISTRIBUTION. The species occurs in Querétaro and Hidalgo (Fig. 11), where it is found primarily in limestone crevices in pine-oak woodland along the Sierra Madre Oriental (Dixon et al., 1972; Taylor, 1939; R.L. Bezy and colleagues, personal observations). It has also been found on an adobe wall in thorn scrub in the Jalpan Valley, Querétaro (Dixon et al., 1972), and in a cave in xerophytic scrub near the Río Tula, Hidalgo (González, 1995). It occurs in sympatry with *L. sylvaticum* and *L. occulor* in Querétaro. A captive female gave birth to one young in March (Dixon et al., 1972). The species appears to be diurnal based on metabolic data (Mautz, 1979) and it is more resistant to water loss than is *L. smithii* (Mautz, 1982).

REMARKS. The populations found in the Jalpan Valley differ slightly in scalation (Bezy and Camarillo, 1992).

ETYMOLOGY. The name *gaigeae* is a noun in the genitive singular case and honors Helen Thompson Gaige (1890–1976), former curator at the University of Michigan Museum of Zoology.

COMMON NAMES. Gaige's Tropical Night Lizard; Lagartija Nocturna de Gaige.

Lepidophyma lineri Smith

Group S1; Figure 17

Lepidophyma flavimaculatum lineri Smith, 1973: 118, Plates 1–2. Holotype: UCM 48452; type lo-



Figure 16 Living individual of *Lepidophyma gaigeae* (ENEPI 4088; snout-vent length, 63 mm).

cality, "Cafetal Pacífico, 2.1 mi. N and 0.4 mi. E Candelaria Loxicha, Oaxaca, on the trail to Cafetal Hedweges (about 17 km. N Pochutla)."

DIAGNOSTIC CHARACTERS. The species differs from all other *Lepidophyma* except *L. smithii* and *L. tarascae* in lacking a pale parietal spot; from *L. smithii* in having 23 or more lateral tubercle rows; from *L. tarascae* in having 179 or more dorsals and 51 or more gulars; from *L. occulor* in having 53 or fewer gulars and 184 or fewer dorsals; from all except *L. dontomasi*, *L. smithii*, *L. tarascae*, and *L. occulor* in having 17 or fewer total femoral pores; and from all except *L. radula*, *L. smithii*, *L. tarascae*, *L. flavimaculatum*, *L. occulor*, and *L. sylvaticum* in having 24 or fewer lateral tubercle rows (Table 1).

KARYOTYPE. Unknown.

SIZE. The maximum snout-vent length for the two undamaged specimens examined is 37 mm.

SEX RATIO. Both specimens sexed are males.

DISTRIBUTION, HABITAT, AND NATURAL HISTORY. The species is known only from the type locality and nearby Cafetal Alemania in the Sierra de Miahuatlán of Oaxaca (Fig. 12).

REMARKS. *Lepidophyma lineri* is most similar to *L. smithii*. Additional material is needed to clarify its variation, distribution, and geographic relationship with *L. smithii*, which occurs ca. 80 km to the west along road to Puerto Escondido, Oaxaca.

ETYMOLOGY. The name *lineri* is a noun in the genitive singular case and honors Ernest A. Liner, one of the herpetologists who collected the holotype.

COMMON NAMES. Liner's Tropical Night Lizard; Lagartija Nocturna de Liner.

Lepidophyma lipetzi Smith and
Álvarez del Toro
Group F2; Figure 18

Lepidophyma lipetzi Smith and Álvarez del Toro, 1977:37, Figs. 2–4. Holotype: UCM 51425; type locality, "Lago de Mal Paso, headwaters of Río de La Venta, 30 km N Cintalapa (straight line), Chiapas, México."

DIAGNOSTIC CHARACTERS. The species differs from all other *Lepidophyma* except *L. smithii*, *L. lineri*, *L. tuxtlae*, *L. chicoasense*, *L. flavimaculatum*, *L. reticulatum*, *L. micropholis*, *L. occulor*, and *L. sylvaticum* in having 46 or more gulars; from *L. micropholis* and *L. occulor* in having 52 or fewer gulars; from all except *L. mayae*, *L. pajapanense*, *L. chicoasense*, *L. flavimaculatum*, *L. reticulatum*, *L. micropholis*, and *L. sylvaticum* in having 35 or more femoral pores; from all except *L. gaigeae*, *L. smithii*, *L. pajapanense*, *L. tuxtlae*, *L. chicoasense*, *L. flavimaculatum*, and *L. reticulatum* in having 6 or more pretympans; from *L. chicoasense* in having 28 or fewer fourth toe la-

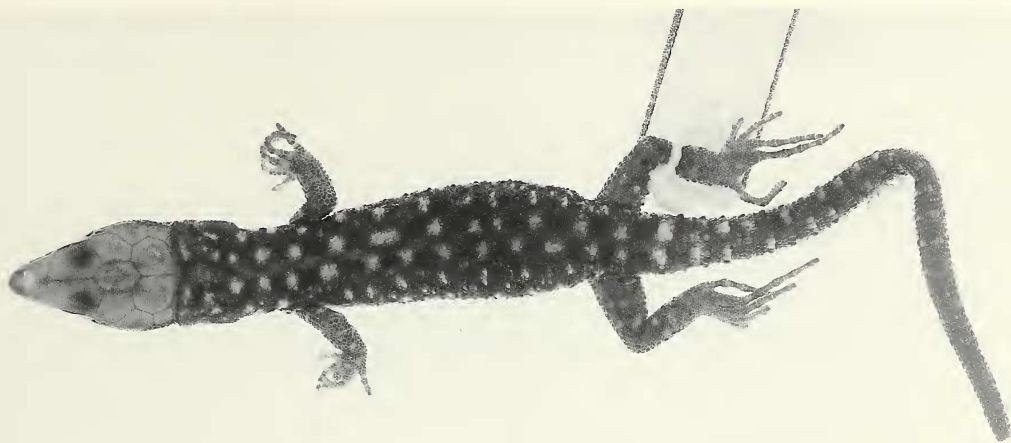


Figure 17 The holotype of *Lepidophyma lineri* (UCM 48452; snout-vent length, 36 mm).

mellae; from *L. reticulatum* in having 35 or more femoral pores, 14 or fewer divided fourth toe lamellae, and 179 or fewer dorsals; and from *L. flavimaculatum* in having 179 or fewer dorsals (99.3% of all *L. flavimaculatum*, 100% of Chiapas specimens; Table 1) and a pale dorsal color pattern (Fig. 18).

KARYOTYPE. Unknown.

SIZE. The maximum snout-vent length for the two specimens examined is 55 mm.

SEX RATIO. Unknown

DISTRIBUTION, HABITAT, AND NATURAL HISTORY. The species is known only from the type locality (Fig. 11), where it occurs with *L. flavimaculatum*. The 2 known specimens were collected on the walls of caves (Smith and Álvarez del Toro, 1977).

REMARKS. The distributional relationship in Chiapas of *L. lipetzi*, found on the Río de La Venta, and *L. chicoasense*, known only from the Cañón Sumidero of the Río Grijalva, may never be resolved because the vast Lago Netzahualcóyotl now lies at the confluence of these rivers.

ETYMOLOGY. The name *lipetzi* is a noun in the genitive singular case and honors Milton L. Lipetz, a University of Colorado faculty member admired by Hobart Smith.

COMMON NAMES. Lipetz's Tropical Night Lizard; Lagartija Nocturna del Ocote.

Lepidophyma lowei Bezy and Camarillo
Group L; Figure 19

Lepidophyma lowei Bezy and Camarillo, 1997:1, Figs. 1–3. Holotype: IBH 7500; type locality, “4.0 km (by rd) SE San Bartolomé Zoogocho, Municipio Zoogocho, former Distrito Villa Alta, Oaxaca, México (17°14'N, 96°15'W; ca. 2200 m elev.).”

DIAGNOSTIC CHARACTERS. The species dif-

fers from all other *Lepidophyma* except *L. dontomasi* and *L. radula* in having enlarged caudal whorls that are separated dorsally by 2 rows of interwhorls, only one of which is complete ventrally; from all except *L. dontomasi*, *L. gaigeae*, *L. radula*, *L. tuxtlae*, and *L. pajapanense* in having 37 or fewer gulars; from *L. dontomasi*, *L. gaigeae*, and *L. radula* in having 158 or more dorsals; and from *L. tuxtlae*, *L. pajapanense*, *L. mayae*, *L. chicoasense*, *L. lipetzi*, *L. flavimaculatum*, *L. reticulatum*, and *L. micropholis* in having 7 or fewer divided fourth toe lamellae (Table 1).

KARYOTYPE. *Lepidophyma lowei* has a diploid chromosome number of 36 with 16 macrochromosomes and 20 microchromosomes (Bezy and Camarillo, 1997). The karyotype appears virtually identical to that of *L. smithii*.

SIZE. The maximum snout-vent length for the 16 specimens examined is 60 mm.

SEX RATIO. Of the 10 specimens sexed, 6 (60%) are males.

DISTRIBUTION, HABITAT, AND NATURAL HISTORY. The species is known only from the vicinity of the type locality (Fig. 11), where it is found in rock crevices in pine-oak woodland. A female gave birth to four offspring in April (Camarillo, 1999).

REMARKS. Additional work is needed to establish the geographic distribution of the species.

ETYMOLOGY. The name *lowei* is a noun in the genitive singular case and honors Charles H. Lowe, a herpetologist at the University of Arizona.

COMMON NAMES. Lowe's Tropical Night Lizard; Lagartija Nocturna de Lowe.

Lepidophyma mayae Bezy
Group T1; Figure 20

Lepidophyma mayae Bezy, 1973:1, Figs. 1–3. Holotype: KU 59554; type locality, “near Chinajá, elev. 140 m., Depto. Alta Verapaz, Guatemala.”

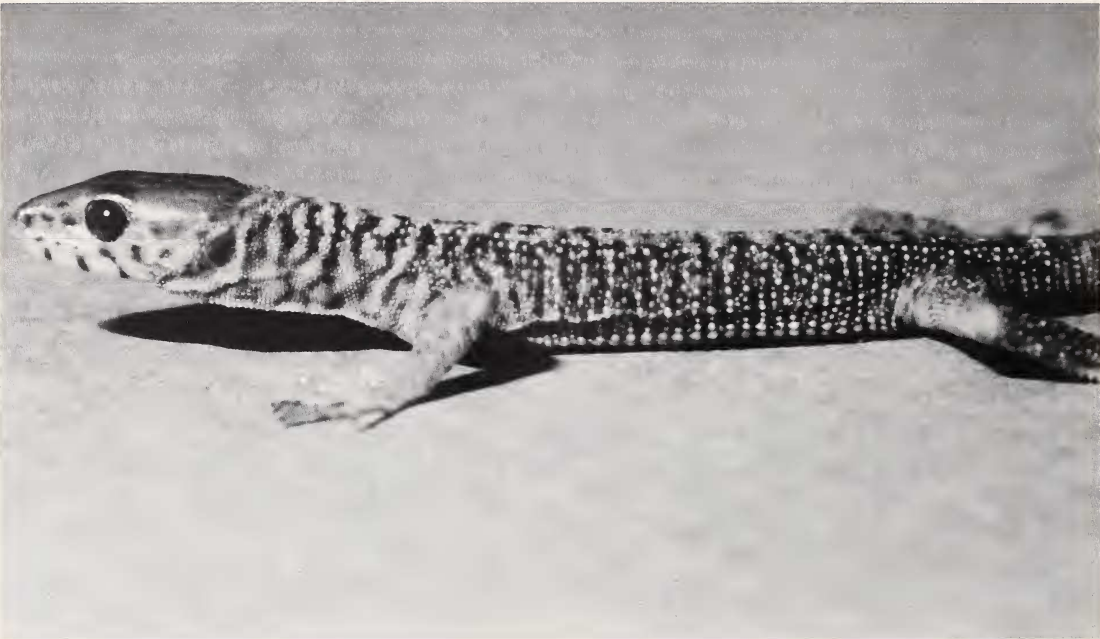


Figure 18 Living individual of *Lepidophyma lipetzi* (ENEPI 3792; snout-vent length, 53 mm).

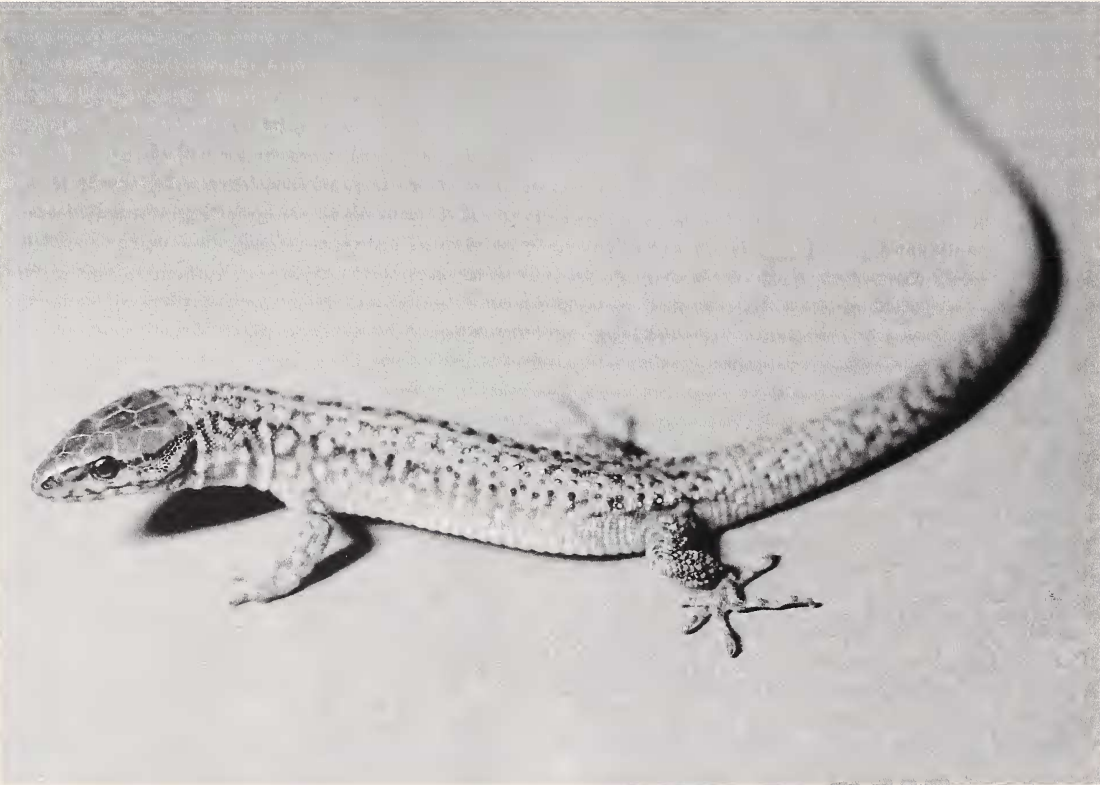


Figure 19 Living individual of *Lepidophyma lowei* (IBH 7500; snout-vent length, 53 mm).



Figure 20 Living individual of *Lepidophyma mayae* (UTA-R 38022; snout-vent length, 78 mm).

DIAGNOSTIC CHARACTERS. The species differs from *L. radula*, *L. tarascae*, *L. lineri*, *L. pajapanense*, *L. tuxtlae*, *L. chicoasense*, *L. lipetzi*, and *L. reticulatum* in having 2 or fewer pretympans; from *L. dontomasi*, *L. gaigeae*, *L. radula*, and *L. tarascae* in having 162 or more dorsals; from *L. reticulatum*, *L. micropholis*, and *L. occulor* in having 188 or fewer dorsals; from *L. lowei*, *L. radula*, *L. smithii*, *L. tarascae*, *L. lineri*, *L. chicoasense*, and *L. occulor* in having 33 or more lateral tubercle rows; from *L. sylvaticum* in having a wider median prefrontal (RMW2 greater than 1.6); and from *L. flavimaculatum* in having 33 or more lateral tubercle rows and two or fewer pretympans (99.6% of all *L. flavimaculatum*, 100% of Guatemalan specimens; Table 1).

KARYOTYPE. Unknown.

SIZE. The maximum snout-vent length for the 16 specimens examined is 75 mm.

SEX RATIO. Of the 10 specimens sexed, 4 (40%) are males.

DISTRIBUTION, HABITAT, AND NATURAL HISTORY. The specimens examined are from 3 areas in Guatemala: the southern El Petén near the base of the Sierra de Chinajá (border of Deptos. El Petén and Alta Verapaz), the Sierra del los Cuchumatanes (Depto. Huehuetenango), and the valley of the Río Cahabón near the lower slopes of the Sierra

Xucaneb (Finca Volcán, Depto. Alta Verapaz; Fig. 11). They were found in lowland rain forest (Chinajá, 140 m; Duellman, 1963) and in an area supporting cloud forest (Finca Chiblac, ca. 1300 m.; Wake and Elias, 1983). At Chinajá the specimens were taken within the rain forest under rocks and logs or active on the forest floor during the day (W.E. Duellman, 1960 field notes). The species is sympatric with *L. flavimaculatum* at Chinajá and Finca Volcán.

Recently, Campbell (1998) recorded the species from additional localities in the Montañas del Mico, Sierra de Santa Cruz, and Maya Mountains north into Belize. The specimens were found in tropical and subtropical wet forest in limestone crevices and under rocks and logs.

REMARKS. Although *Lepidophyma mayae* can be distinguished from all *L. flavimaculatum* only by a combination of 2 characters (lateral tubercle rows and pretympans), where the two species are found in sympatry each of the two characters is nonoverlapping, indicating reproductive isolation.

ETYMOLOGY. The name *mayae* is a noun in the genitive singular case and refers to the Maya, the indigenous people of the region of the type locality.

COMMON NAMES. Mayan Tropical Night Lizard; Escorpión Nocturno Maya.

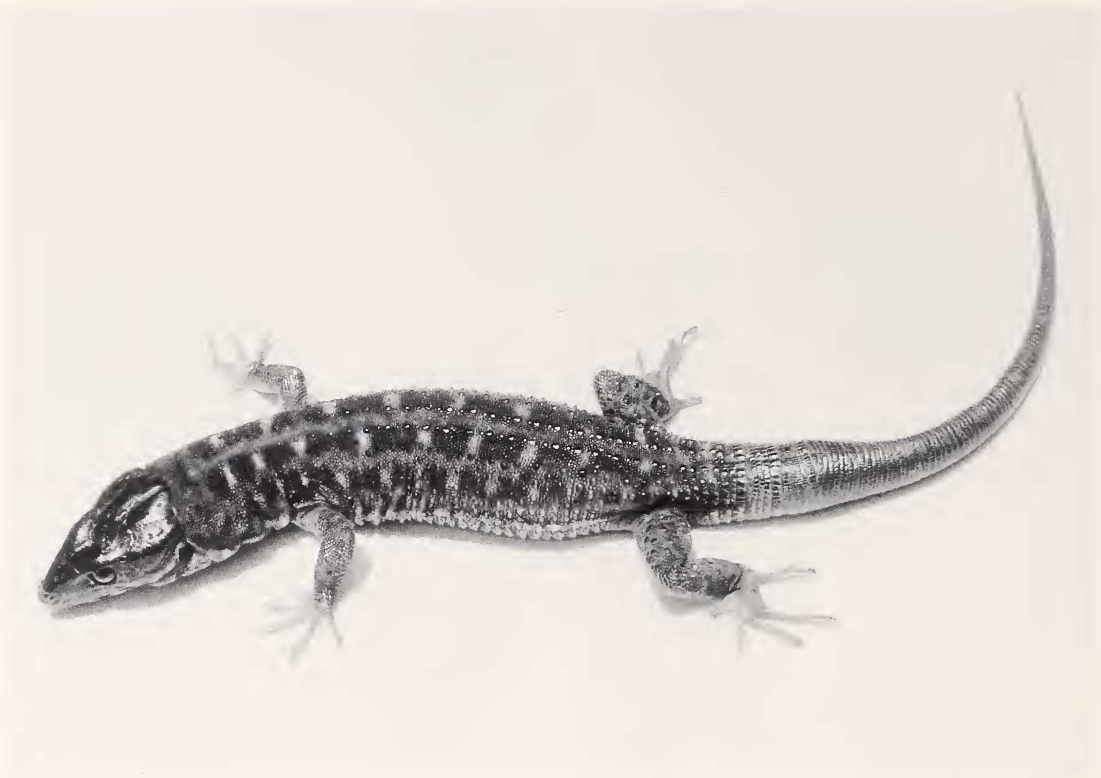


Figure 21 Living individual of *Lepidophyma micropholis* (LACM 106767; snout-vent length, 87 mm).

Lepidophyma micropholis Walker

Figure 21

Lepidophyma micropholis Walker, 1955:6. Holotype: UMMZ 101298; type locality, "cave at El Pachón, about 5 miles NNE of Antigua Morelos, Tamaulipas, estimated elevation 600–700 feet."

DIAGNOSTIC CHARACTERS. The species differs from all other *Lepidophyma* except *L. occulor* in having 230 or more dorsal scales. It differs from *L. occulor*, *L. dontomasi*, *L. radula*, *L. tarascae*, and *L. lineri* in having 28 or more femoral pores; and from all except *L. smithii*, *L. flavimaculatum*, *L. chicoasense*, *L. occulor*, and *L. sylvaticum* in having 55 or more gulars (Table 1).

KARYOTYPE. *Lepidophyma micropholis* has a diploid chromosome number of 36 with 16 macrochromosomes and 20 microchromosomes. The karyotype appears identical to that of *L. sylvaticum*.

SIZE. The maximum snout-vent length for the 31 specimens examined is 111 mm.

SEX RATIO. Of the 23 specimens sexed, 12 (52%) are males.

DISTRIBUTION, HABITAT, AND NATURAL HISTORY. The species is known from four localities in Sierra del Abra of Tamaulipas and San Luis Potosí (Fig. 11) where it is found in limestone caves and crevices. The vegetation near the type locality

consists of tropical deciduous forest. Within the caves, the lizards have been observed active during the day near the mouth, where they are found on ledges and in crevices in the walls and mud floor (Walker, 1955; R.L. Bezy and colleagues, personal observations).

REMARKS. *Lepidophyma micropholis* appears to be a facultative troglodyte, because a number of individuals have been observed to be active outside caves (J.R. Dixon, personal communication).

ETYMOLOGY. The name *micropholis* (Greek: *mikros*, small; *pholis*, scale) is a noun in apposition and presumably refers to the small size of the dorsal scales.

COMMON NAMES Cave Tropical Night Lizard; Lagartija Nocturna de Cueva.

Lepidophyma occulor Smith

Figure 22

Lepidophyma smithii occulor Smith, 1942:378. Holotype: USNM 47133; type locality, "Jalpan, Querétaro."

Lepidophyma flavimaculatum occulor: Walker, 1955:5.

Lepidophyma occulor: Bezy, 1972:15.

DIAGNOSTIC CHARACTERS. The species dif-

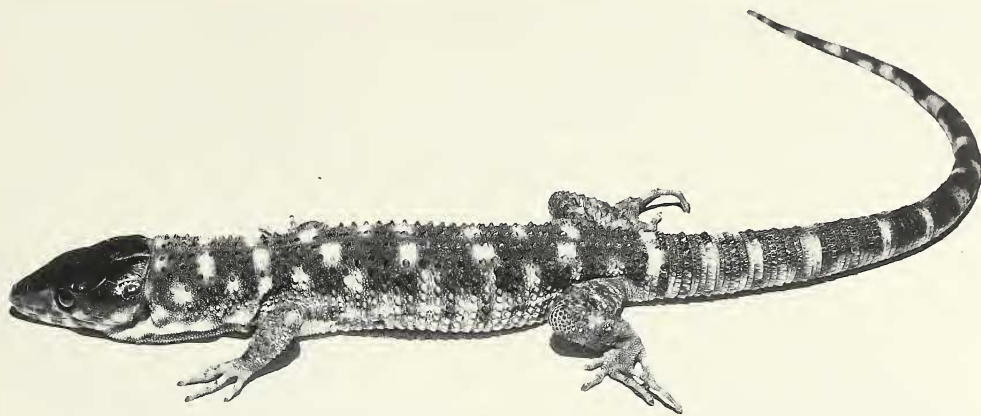


Figure 22 Living individual of *Lepidophyma occulor* (TCWC 35605; snout-vent length, 90 mm).

fers from all other *Lepidophyma* except *L. smithii* and *L. micropholis* in having 58 or more gulars; from all except *L. radula*, *L. smithii*, *L. lineri*, *L. tarascae*, *L. flavimaculatum*, and *L. sylvaticum* in having 25 or fewer lateral tubercle rows; and from *L. smithii* in having 22 or more lateral tubercle rows (99%; Table 1) and in having a pale parietal spot throughout life.

KARYOTYPE. *Lepidophyma occulor* has a diploid chromosome number of 36 with 18 macrochromosomes and 18 microchromosomes (Bezy, 1972). The karyotype is unique within the Xantusiidae.

SIZE. The maximum snout-vent length for the 11 specimens examined is 105 mm.

SEX RATIO. Of the 11 specimens sexed, 7 (64%) are males.

DISTRIBUTION, HABITAT, AND NATURAL HISTORY. The species occurs in thorn scrub in the Jalpan valley of Querétaro and San Luis Potosí (Fig. 11), where the lizards have been found under rocks or active at night near limestone outcrops and in rock walls and ruins (Dixon et al., 1972; R.L. Bezy and J.L. Camarillo, personal observations). East of the Jalpan region, it has been taken in a cave in tropical forest along the Río Moctezuma near Tamazunchale, San Luis Potosí (Camarillo, 1993). It occurs in sympatry with *L. gaigeae*.

REMARKS. *Lepidophyma occulor* is most similar to *L. smithii*, from which it differs in karyotype and in the presence of a parietal spot.

ETYMOLOGY. The name *occulor* (Latin: one who hides) is a noun in apposition and refers to the

secretive or reclusive behavior of the members of the genus (H.M. Smith, personal communication).

COMMON NAMES. Jalpan Tropical Night Lizard; Lagartija Nocturna de Jalpan.

Lepidophyma pajapanense Werler Group T2; Figure 23

Lepidophyma pajapanensis Werler, 1957:223, Plate 1, Fig. 1. Holotype: FMNH 78382; type locality, "southeast slopes of Volcán San Martín Pajapán, Veracruz, México; elevation 3,500 feet."

Lepidophyma pajapanense: Pérez-Higareda, 1978: 69.

DIAGNOSTIC CHARACTERS. The species differs from all other *Lepidophyma* except *L. tuxtlae* in having the paravertebral rows composed of a nearly uninterrupted string of subequal tubercles; from *L. tuxtlae*, *L. dontomasi*, *L. gaigeae*, *L. radula*, *L. tarascae*, *L. lineri*, and *L. occulor* in having 30 or more femoral pores; from all except *L. mayae*, *L. tuxtlae*, and *L. sylvaticum* in having 39 or more large paravertebral tubercles; and from *L. dontomasi*, *L. lowei*, *L. radula*, *L. tarascae*, *L. lineri*, *L. mayae*, *L. micropholis*, *L. occulor*, and *L. sylvaticum* in having 6 or more pretympanics (Table 1)

KARYOTYPE. *Lepidophyma pajapanense* has a diploid chromosome number of 38 with 18 macrochromosomes and 20 microchromosomes (Bezy, 1972). The karyotype appears to be identical to that of *L. tuxtlae*, *L. flavimaculatum*, and *L. reticulatum*.



Figure 23 Living individual of *Lepidophyma pajapanense* (LACM 135510; snout–vent length, 57 mm).

SIZE. The maximum snout–vent length for the 22 specimens examined is 82 mm.

SEX RATIO. Of the 16 specimens sexed, 5 (31%) are males.

DISTRIBUTION, HABITAT, AND NATURAL HISTORY. The species is known only from Veracruz and occurs in the Sierra de Los Tuxtlas (Volcán San Martín Tuxtla to Volcán San Martín Pajapán) and from the vicinity of the Río Coatzacoalcos near Jesús Carranza on the Isthmus of Tehuantepec. It is sympatric with *L. tuxtlae* in the Tuxtlas region, and with *L. tuxtlae* and *L. flavimaculatum* near the Río Coatzacoalcos (Fig. 11). The locality data for the specimen reported from Huayacacotla, Veracruz (Aguilar Cortés et al., 1990), is now considered questionable because extensive collecting in the area has yielded numerous *L. sylvaticum*, but no additional specimens of *L. pajapanense*.

In the Tuxtlas the lizards are nocturnal and found beneath the bark and between the buttresses of trees within the rain forest from sea level to 1500 m (Vogt et al., 1997). Both *L. pajapanense* and *L. tuxtlae* have been taken from the same tree stump in recent clearings near the forest edge in the Tuxtlas (R.L. Bezy and C.J. Cole, personal observations).

The male and female reproductive cycles are asynchronous and four to eight young are born in

late May or early June (Méndez-de la Cruz et al., 1999).

REMARKS. This morphologically distinctive species has a rather restricted distribution, which fortunately includes the preserve at Estación de Biología Tropical “Los Tuxtlas.”

ETYMOLOGY. The name *pajapanense* is an adjective and refers to the type locality, Volcán San Martín Pajapán. The original name was justifiably emended by Pérez-Higareda (1978) to modify the neuter generic name.

COMMON NAMES. Pajapan Tropical Night Lizard; Lagartija Nocturna de Pajapán.

Lepidophyma radula (Smith)

Group R; Figure 24

Gaigeia radula Smith, 1942:374. Holotype: USNM 111472; type locality, “San José Manteca, 5 kilometers from San Carlos Yautepec, Oaxaca.”

Lepidophyma radula: Savage, 1963:35.

DIAGNOSTIC CHARACTERS. The species differs from all other *Lepidophyma* except *L. dontomasi* and *L. lowei* in having enlarged caudal whorls that are separated dorsally by 2 rows of interwhorls, only one of which is complete ventrally; from all except *L. gaigeae* and *L. dontomasi* in having less than 140 dorsals; from *L. dontomasi* in

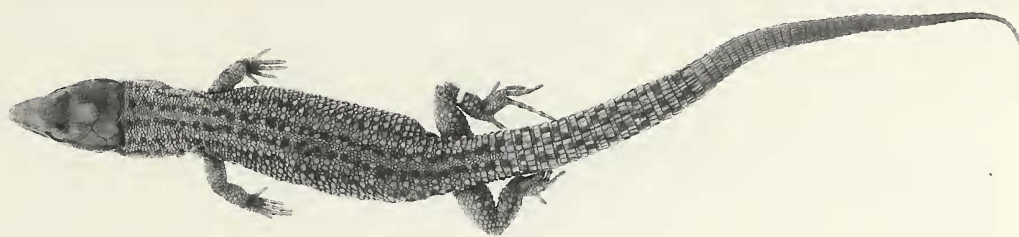


Figure 24 The holotype of *Lepidophyma radula* (USNM 111472; snout-vent length, 41 mm).

having distinctly enlarged tubercles on the side of the body; and from *L. lowei* and *L. gaigeae* in having fewer than 22 femoral pores (Table 1).

KARYOTYPE. Unknown.

SIZE. The snout-vent length of the only known specimen is 41 mm.

SEX RATIO. The holotype is a female.

DISTRIBUTION, HABITAT, AND NATURAL HISTORY. The species is known only from the type locality (Fig. 11), where the vegetation consists of tropical deciduous forest.

REMARKS. *Lepidophyma radula* remains known only from the holotype. Considerable field work conducted by the authors in the region of the type locality has failed to produce additional specimens. *Lepidophyma smithii* occurs nearby (Portillo Nejapa, Oaxaca) and differs extensively in sculation.

Lepidophyma dontomasi, *L. lowei*, and *L. radula* are restricted to eastern Oaxaca and are unique in the genus in having most caudal whorls separated by only 2 interwhorls, one of which is complete ventrally.

ETYMOLOGY. The name *radula* (Latin: scraper) is a noun in apposition and refers to the body surface, which is rough, or filelike because of the presence of large tubercular scales (H.M. Smith, personal communication).

COMMON NAMES. Yauatepec Tropical Night Lizard; Lagartija Nocturna de Yauatepec.

Lepidophyma reticulatum Taylor

Group F3; Figures 25, 26

Lepidophyma reticulatum Taylor, 1955:551, Fig. 14. Holotype: KU 36245; type locality, "Agua Buena, Puntarenas Province, Costa Rica."

Lepidophyma flavimaculatum reticulatum: Wermuth, 1965:196.

DIAGNOSTIC CHARACTERS. The species differs from all other *Lepidophyma* except *L. smithii*, *L. flavimaculatum*, *L. lipetzi*, *L. micropholis*, *L. occulor*, and *L. sylvaticum* in having 193 or more dorsals; from *L. micropholis* in having 229 or fewer dorsals; from *L. dontomasi*, *L. radula*, *L. tarascae*, *L. lineri*, and *L. occulor* in having 27 or more fem-

oral pores; from *L. lipetzi* in having 33 or fewer femoral pores; from *L. smithii*, *L. tarascae*, *L. lineri*, and *L. occulor* in having 28 or more lateral tubercle rows; from *L. sylvaticum* in having a lower second postorbital supralabial (RSLH 0.71 or less; Table 1); and from *L. flavimaculatum* in having a boldly reticulated color pattern on the gular surface (Fig. 26).

KARYOTYPE. *Lepidophyma reticulatum* has a diploid chromosome number of 38 with 18 macrochromosomes and 20 microchromosomes (Bezy, 1972, as *L. flavimaculatum*). The karyotype appears to be virtually identical to that of *L. pajapanense*, *L. tuxtlae*, and *L. flavimaculatum*.

SIZE. The maximum snout-vent length for the 65 specimens examined is 103 mm.

SEX RATIO. No males are present among 29 specimens sexed.

DISTRIBUTION, HABITAT, AND NATURAL HISTORY. *Lepidophyma reticulatum* ranges on the Pacific slope of Costa Rica from the area of Tilarán (Guanacaste Province) to the Península de Osa and San Vito de Java (Puntarenas Province; Fig. 12). In the Tilarán area it occurs in sympatry with a population of *L. flavimaculatum* that includes males. The species has been collected within and under decaying logs and beneath rocks (R.L. Bezy and K. Bolles, personal observations).

REMARKS. This unisexual species may range into southwestern Panamá.

ETYMOLOGY. The name *reticulatum* (Latin: netlike or reticulated) is an adjective and refers to the gular color pattern.

COMMON NAMES. Costa Rican Tropical Night Lizard; Lagartija Nocturna de Costa Rica.

Lepidophyma smithii Bocourt

Groups S2, S3; Figure 27

Lepidophyma smithii Bocourt, 1876:402. Syntypes: MNHN 76.95, 4323, A4323, B4323, 4968, A4968; type locality, "Tehuantepec" and "Guatemala occidental" (restricted to Guatemala by Smith, 1942, and to Mazatenango by Smith and Taylor, 1950).

Akilestrops guatemalensis Muller, 1877:390, Tafel I,

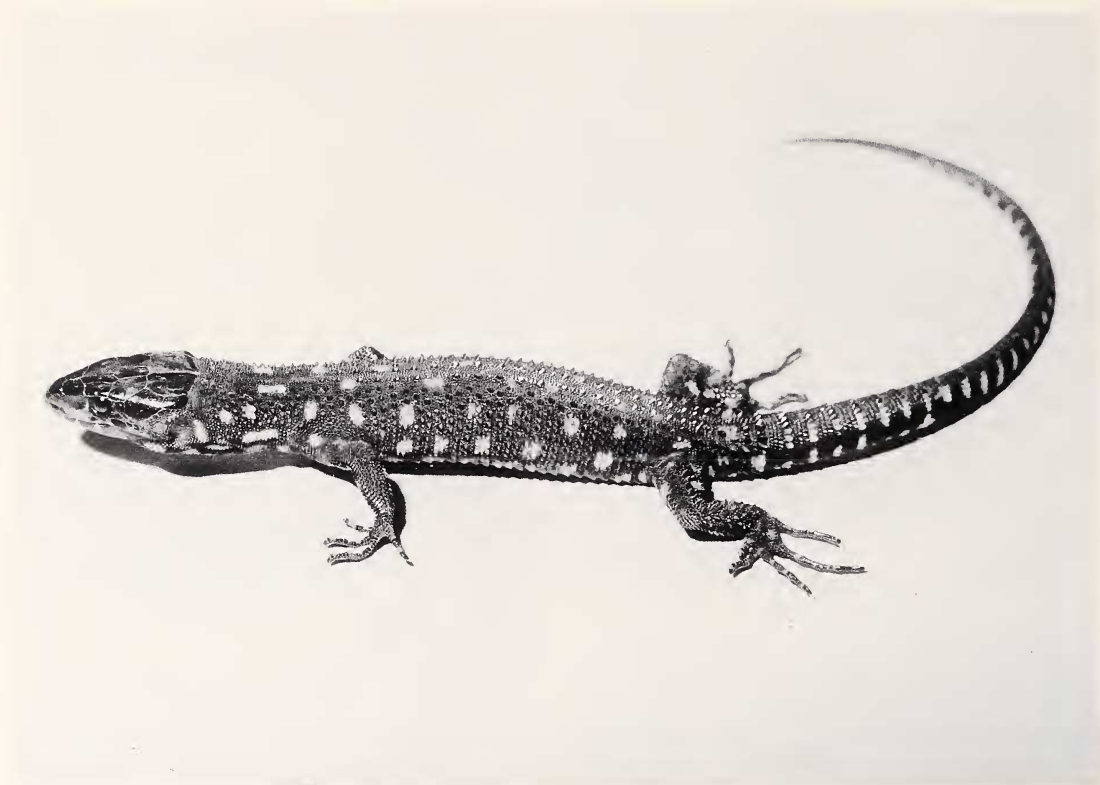


Figure 25 Living individual of *Lepidophyma reticulatum* (LACM; snout-vent length, 90 mm).

II. Syntypes: NMBA 3748–50, 3752, 8039–40; type locality, “Mazatenango (costa grande von Guatemala).”

Lepidophyma smithii tehuanae Smith, 1942:377.
Holotype: USNM 111488; type locality, “Cerro

Arenal, 30 kilometers west of Tehuantepec, Oaxaca.”

Lepidophyma smithii smithii: Smith, 1942:380.

Lepidophyma flavimaculatum smithii: Walker, 1955:5.

DIAGNOSTIC CHARACTERS. The species differs from all other *Lepidophyma* except *L. tarascae* and *L. lineri* in lacking a pale spot on the parietal scale in adults (snout-vent length greater than 75 mm); from all except *L. tarascae*, *L. occulor*, and *L. sylvaticum* in having 22 or fewer lateral tubercle rows; and from *L. tarascae* in having 162 or more dorsals and 44 or more gulars (Table 1).

KARYOTYPE. *Lepidophyma smithii* has a diploid chromosome number of 36 with 16 macrochromosomes and 20 microchromosomes (Bezy, 1972). The macrochromosomes are similar to those of *L. dontomasi* (Bezy and Camarillo, 1992), but the 2 species differ in number of microchromosomes (20 vs 16).

SIZE. The maximum snout-vent length for the 291 specimens examined is 112 mm.

SEX RATIO. Of the 234 specimens sexed, 91 (39%) are males.

DISTRIBUTION, HABITAT, AND NATURAL HISTORY. The species ranges along the Pacific versant from Guerrero to El Salvador (Fig. 12). One specimen (TCWC 26716) represents a strange geo-

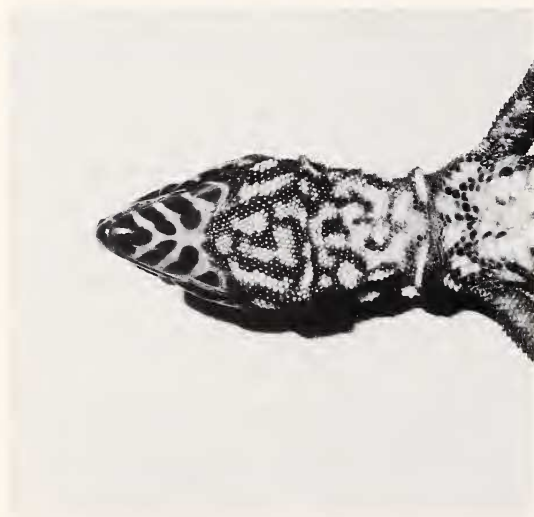


Figure 26 Gular pattern of a living individual of *Lepidophyma reticulatum* (LACM; snout-vent length, 90 mm).

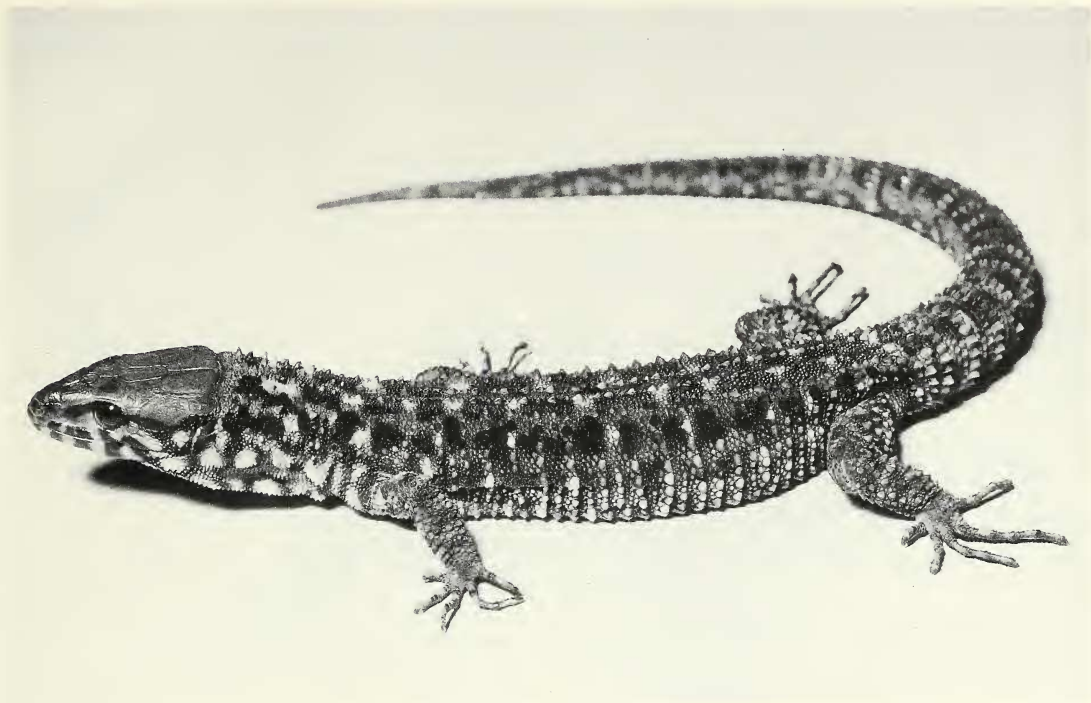


Figure 27 Living individual of *Lepidophyma smithii* (LACM 135511; snout-vent length, 92 mm).

graphical anomaly. The specimen bears a field tag with the locality "2 mi NW Sontecomapan, Veracruz." The species is otherwise unrecorded from the Atlantic versant and no other specimens are present among the many individuals of *L. tuxtlae* and *L. pajapanense* from the Los Tuxtlas region. The specimen is clearly assignable to *L. smithii* (based on femoral pores, lateral tubercle rows, and large paravertebrals; Table 2). It has a parietal spot, a feature that is absent in adult *L. smithii* (Table 2), but the snout-vent length (41 mm) of the specimen is within the range of the few juvenile *L. smithii* in which the spot is visible (28–75 mm). The locality is here considered questionable for *L. smithii*, but the possibility that the species occurs in the Tuxtlas cannot be completely ruled out in view of the many biogeographic enigmas presented by xantusiids.

The species occurs in a variety of habitats. At the northernmost known locality, near Puerto Marqués, Guerrero, it occurs in a system of caves formed by piles of large granitic boulders in tropical semideciduous forest. Within the caves, the lizards have been found to be active day and night in both the dry and wet seasons, to evidence territoriality, and to consume the fruit of native figs, *Ficus petiolaris* (Mautz, 1976, 1982; Mautz and López-Forment, 1978). In Oaxaca, specimens have been found in logs and rock crevices on Cerro Quiengola (Hartweg and Oliver, 1940), and in caves and road culverts on the Isthmus of Tehuantepec (R.L. Bezy and colleagues, personal observations); in Chiapas,

in logs and tree stumps in savanna (R.L. Bezy and colleagues, personal observations); and in Guatemala, on the rain forest floor and in rotting logs where the stomachs of specimens contained termites (Slevin, 1942, as *L. flavomaculatum*).

REMARKS. Walker (1955) concluded that *L. smithii* is conspecific with *L. flavimaculatum* and this arrangement has been followed by several subsequent workers (e.g., Smith, 1973). The ranges of the two forms are separated by only ca. 20 km on the Isthmus of Tehuantepec, with *L. smithii* extending north to Santo Domingo de Guzmán (= Santo Domingo Petapa; Goodwin, 1969) and *L. flavimaculatum* south to El Mogoñé. In this region, the two species differ in number of femoral pores, lateral tubercle rows, and the presence of a pale interparietal spot. Although geographical variation among the localities of these 2 widely distributed species produces overlap in number of femoral pores, the two species consistently differ in two other scale features (Table 1) and in chromosome number (Bezy, 1972).

The population of *L. smithii* found near Puerto Marqués, Guerrero, is the most divergent in scalation and its systematic status warrants further study.

ETYMOLOGY. The name *smithii* is a noun in the genitive singular case and honors Sir Andrew Smith, M.D. (1797–1872; founder of the South African Museum), whose description and figure of *Poriodogaster grayi* (a junior synonym of *L. flavi-*

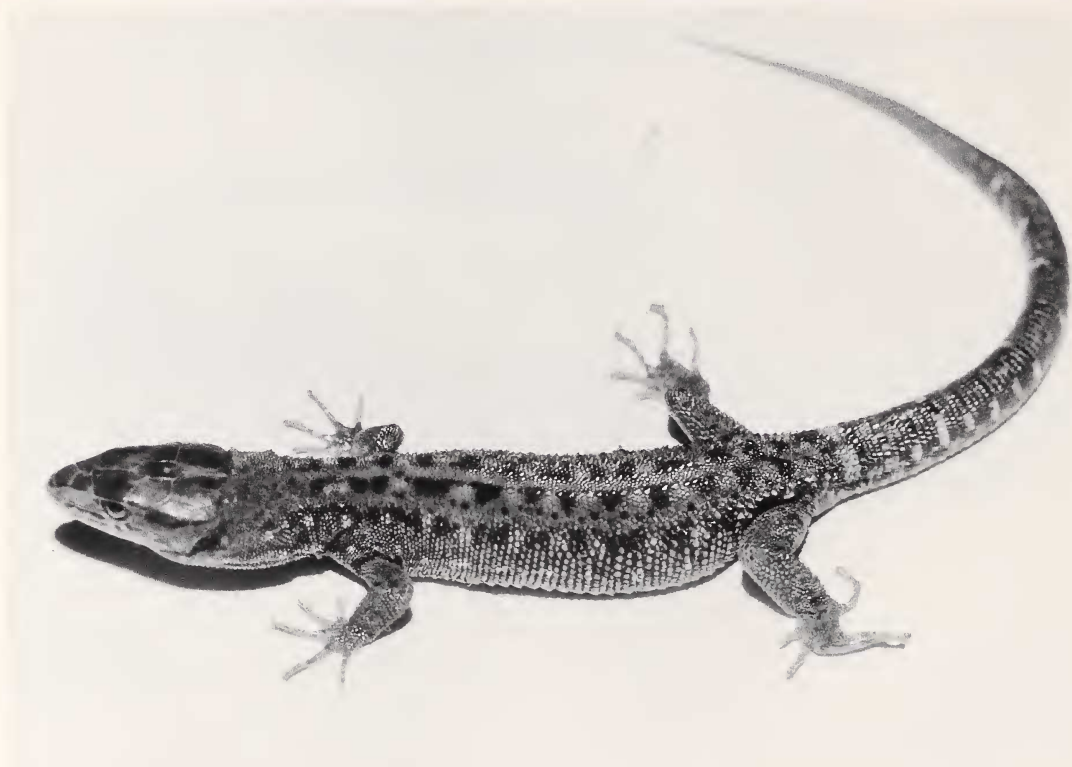


Figure 28 Living individual of *Lepidophyma sylvaticum* (LACM 106744; snout-vent length, 75 mm).

maculatum) was used by Bocourt (1876) to compare with *L. smithii*.

COMMON NAMES. Smith's Tropical Night Lizard; Lagartija Nocturna de Smith.

Lepidophyma sylvaticum Taylor

Figure 28

Lepidophyma sylvatica Taylor, 1939:1, Figs. 1, 2. Holotype: FMNH 100102 (EHT-HMS 16259); type locality, "7 mi. north of Zacualtipán, Hidalgo."

Gaigeia sylvatica: Smith, 1942:380.

Lepidophyma sylvaticum: Walker, 1955:9.

Lepidophyma flavimaculatum tenebrarum Walker, 1955:1. Holotype: UMMZ 101374; type locality, "± 5 miles NW (by road) of Gómez Farías, in the Sierra Madre Oriental at 'Rancho del Cielo,' + 3600 feet."

DIAGNOSTIC CHARACTERS. The species differs from *L. dontomasi*, *L. radula*, *L. tarascae*, and *L. lineri* in having 22 or more femoral pores; from *L. gaigeae* in having distinctly enlarged lateral tubercles forming 15 to 38 rows; from *L. tuxtlae* and *L. pajapanense* in having the paravertebral rows composed of tubercles that are heterogeneous in size; from *L. lowei* in having 40 or more gulars; from *L. occulor* in having 56 or fewer gulars; from

L. smithii in having a pale parietal spot throughout life; from *L. lipetzi* and *L. chicoasense* in having four or fewer pretympanics; from *L. micropholis* in having 217 or fewer dorsals; from *L. reticulatum* in having a higher second postorbital supralabial (RSLH of 0.84 or greater); and from *L. flavimaculatum* in having 3 or fewer pretympanics (99.3%) and a higher second supralabial (RSLH of 0.84 or greater; 99.3%; Table 1).

KARYOTYPE. *Lepidophyma sylvaticum* has a diploid chromosome number of 36 with 16 macrochromosomes and 20 microchromosomes. A microchromosomal heteromorphism was found in some individuals from Sierra de Cucharas (Bezy, 1984).

SIZE. The maximum snout-vent length for the 110 specimens examined is 113 mm.

SEX RATIO. Of the 86 specimens sexed, 24 (28%) are males. Males appear to be rare in the populations found in the Sierra de Cucharas, Tamaulipas (3/29; 10%), and at El Lobo, Querétaro (2/13; 15%).

DISTRIBUTION, HABITAT, AND NATURAL HISTORY. The species is found along the Sierra Madre Oriental from Nuevo León to Veracruz (Fig. 12). Outlying populations occur in canyons below the Cumbre de Monterey (Nuevo León), in the Sierra de Tamaulipas (Tamaulipas), the Sierra Álvarez (San Luis Potosí), and near Tlapacoyan and Al-

varado, Veracruz. It has recently been reported from Puebla, near Tepango de Rodríguez (Camarillo, 1995), and in the Sierra Norte (Canseco-Marquéz et al., 2000). The species occurs primarily in pine-oak woodland, humid pine forest, and cloud forest where it is found under bark, logs, and limestone rocks; and in rock crevices, walls, and buildings (Canseco-Marquéz et al., 2000; Dixon et al., 1972; Martin, 1958; Walker, 1955; R.L. Bezy and J.L. Camarillo, personal observations). It is sympatric with *L. gaigeae* in Querétaro.

REMARKS. The occurrence of *L. sylvaticum* at Alvarado on the coast of Veracruz is somewhat enigmatic and brings the range of the species to within ca. 85 km of that of *L. flavimaculatum*. The two species appear to maintain their morphological differences in this area, with the Alvarado specimen (MZFC 1722) differing from the northernmost *L. flavimaculatum* (ENEPI 2104 from the Tuxtla region) in pretympans (2 vs 4) and the height of the second postorbital supralabial (RSLH 0.98 vs. 0.58).

Within *L. sylvaticum*, the morphologically most distinctive group of populations is composed of the samples from widely disjunct localities in the Sierra Álvarez of San Luis Potosí and in the northern base of the Sierra Madre Oriental of Nuevo León.

ETYMOLOGY. The name *sylvaticum* (Latin: of woods) is an adjective and presumably refers to the occurrence of the species in humid pine and fir forest.

COMMON NAMES. Madrean Tropical Night Lizard; Lagartija Nocturna de Montaña.

Lepidophyma tarascae Bezy, Webb,
and Álvarez
Group S1; Figure 29

Lepidophyma tarascae Bezy, Webb, and Álvarez, 1982:1, Figs. 1–3. Holotype: IPN 9221; type locality, “near Mexiquillo, Aquila District, Michoacán, México.”

DIAGNOSTIC CHARACTERS. The species differs from all other *Lepidophyma* except *L. smithii* and *L. lineri* in lacking a pale parietal spot in adults; from *L. smithii*, *L. lineri*, and *L. occulor* in having 159 or fewer dorsals and 43 or fewer gulars; from all except *L. dontomasi*, *L. smithii*, *L. lineri*, *L. tuxtlae*, and *L. occulor* in having 18 or fewer total femoral pores; and from all except *L. radula*, *L. smithii*, *L. lineri*, *L. flavimaculatum*, *L. occulor*, and *L. sylvaticum* in having 25 or fewer lateral tubercle rows (Table 1).

KARYOTYPE. Unknown.

SIZE. The maximum snout-vent length for the 4 specimens examined is 93 mm.

SEX RATIO. Of the 4 specimens sexed, 3 (75%) are males.

DISTRIBUTION, HABITAT, AND NATURAL HISTORY. The species is known only from two localities in Michoacán (Fig. 12): the type locality on the Pacific coast and the Cañón del Río Chilitos

in the northern sector of the Sierra Coalcomán (Guzmán-Villa et al., 1998). The type series was reported to have been collected in a rocky ravine in tropical semideciduous forest (Bezy et al., 1982), but Álvarez and Díaz-Pardo (1983) indicated that the specimens were found in encinar (evergreen oak woodland). The specimen from the Río Chilitos was taken from a cave in a transition zone between tropical deciduous forest and oak woodland (Guzmán-Villa et al., 1998).

REMARKS. *Lepidophyma tarascae* is most similar to *L. smithii*, and additional material may bridge the differences between the two in dorsals and gulars. All known specimens of *L. tarascae* have an uninterrupted row of enlarged tubercles extending from the posteroventral margin of the ear opening to above the gular fold (fig. 3 in Bezy et al., 1982). However, in the Coalcomán specimen (MZFC 8603) the row is not as distinct as in the type series (i.e., it is less clearly separated from the scattered large tubercles of the upper nuchal area) and approaches the condition seen in some *L. smithii*.

ETYMOLOGY. The name *tarascae* is a noun in the genitive singular case and refers to the Tarasca, the indigenous people of the region of the type locality (Michoacán).

COMMON NAMES. Tarascan Tropical Night Lizard; Lagartija Nocturna de Tarasca.

Lepidophyma tuxtlae Werler and Shannon
Group T3; Figure 30

Lepidophyma tuxtlae Werler and Shannon, 1957: 119, Plate I. Holotype: UIMNH 67064 (FAS 10550); type locality, “lower slopes of Volcán San Martín, Veracruz, elevation 2,500 feet.”

Lepidophyma flavimaculatum tuxtlae: Savage, 1963:35.

Lepidophyma sawini Smith, 1973:112, Plates 1–2. Holotype: UCM 49280; type locality, “Vista Hermosa, Comaltepec, Ixtlán, Oaxaca, México.”

Lepidophyma alvarezii Smith, 1973:115, Plates 1–2. Holotype: UCM 49281; type locality, “43 km on the road between Ocozocoautla and Mal Paso, 620 m Chiapas.”

DIAGNOSTIC CHARACTERS. The species differs from all other *Lepidophyma* except *L. pajapanense* in having the paravertebral rows composed of a nearly uninterrupted string of subequal tubercles; from *L. pajapanense*, *L. lipetzi*, and *L. chicoasense* in having 29 or fewer femoral pores; from all except *L. mayae*, *L. pajapanense*, *L. lipetzi*, and *L. sylvaticum* in having 30 or more large paravertebrals; and from *L. radula*, *L. smithii*, *L. tarascae*, *L. lineri*, and *L. occulor* in having 30 or more lateral tubercle rows (Table 1).

KARYOTYPE. *Lepidophyma tuxtlae* has a diploid chromosome number of 38 with 18 macrochromosomes and 20 microchromosomes (Bezy, 1972). The karyotype appears to be identical to that of *L. pajapanense*, *L. flavimaculatum*, and *L. reticulatum*.



Figure 29 The holotype of *Lepidophyma tarascae* (IPN 9221; snout-vent length, 93 mm).

SIZE. The maximum snout-vent length for the 97 specimens examined is 97 mm.

SEX RATIO. Of the 82 specimens sexed, 34 (41%) are males. Castillo-Cerón and López-González (1990) found only one male (9%) in the 11 specimens collected at their study site on Volcán Santa Marta, suggesting that the species may have a highly skewed sex ratio at certain localities.

DISTRIBUTION, HABITAT, AND NATURAL HISTORY. The species is known from the Sierra de los Tuxtlas (Zapoapan to Volcán San Martín Tuxtla), Veracruz; the Sierra de Juárez, Oaxaca; the Río Coatzacoalcos and Sierra Atravesada on Isthmus of

Tehuantepec, Veracruz and Oaxaca; and the Selva del Ocote, Chiapas (Fig. 11). It is sympatric with *L. flavimaculatum* in the Río Coatzacoalcos and the Ocote areas and with *L. pajapanense* in the Tuxtlas and Río Coatzacoalcos regions.

Vogt et al. (1997) indicated that in the Tuxtlas the species is nocturnal and inhabits trees within the rain forest from sea level to 1500 m. Individuals have been found within rotting logs and beneath the bark of tree stumps within or near the rain forest (R.L. Bezy and C.J. Cole, personal observations). Greene (1970) reported that a female collected near Lago Catemaco in June contained 6

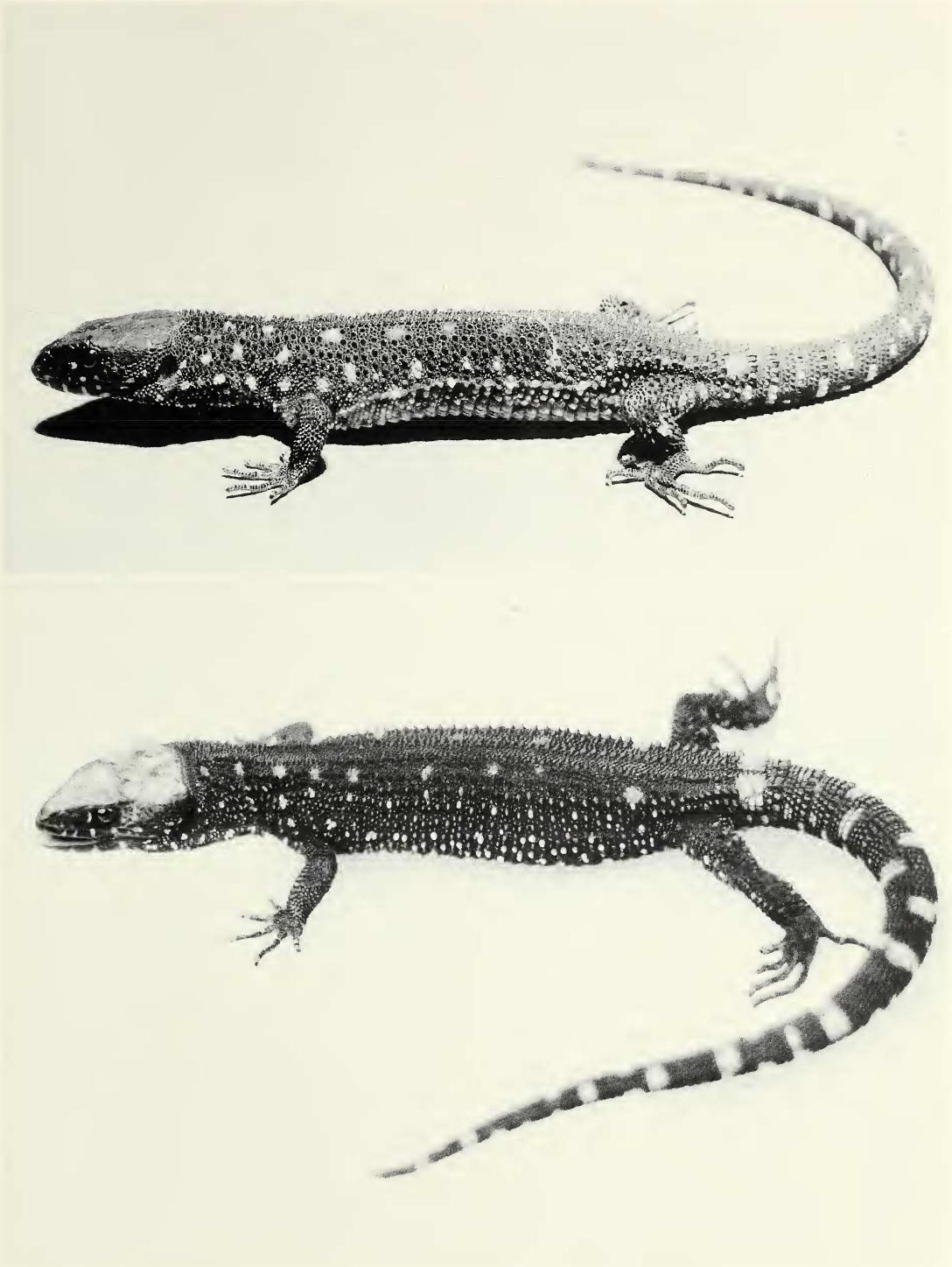


Figure 30 Living individuals of *Lepidophyma tuxtlae* from the Tuxtlas region of Veracruz (upper; LACM 136358; snout-vent length, 62 mm) and the Vista Hermosa region of Oaxaca (lower; UMMZ 125870; snout-vent length, 97 mm; photo by Kraig Adler).

arated dorsally by 4 smaller scale rows
 *L. mayae*

SPECIMENS EXAMINED

The 1,420 specimens of *Lepidophyma* examined are listed below. The numbers (in parentheses) preceding the localities denote separate locality samples used in the analyses of variation. The specimens are listed generally northwest to southeast, with the states of México (Nuevo León, Tamaulipas, San Luis Potosí, Querétaro, Hidalgo, Guerrero, Michoacán, Veracruz, Oaxaca, Tabasco, Chiapas, and Quintana Roo) followed by the countries of Central America. Museum abbreviations follow Leviton et al. (1985) with the addition of: BCB (B.C. Brown collection at the Strecker Museum), CRE (J.M. Savage Costa Rica collection, now at LACM); EAL (E.A. Liner collection, now at AMNH), JFC (J.F. Copp collection, now at CAS); ENEPI (Escuela Nacional Estudios Profesionales, Iztacala, UNAM), MZFC (Museo de Zoología, Facultad de Ciencias, UNAM), OMNH (Oklahoma Museum of Natural History), and SAM (Sherman A. Minton Collection, now at AMNH).

L. chicoasense

CHIAPAS: (1): 16.3 km N, 1.6 km E Tuxtla Gutiérrez (IPN 11130–33).

L. dontomasi

OAXACA: (1): D. Tehuantepec: Lachiguirí: Cerro de Lachiguirí (ENEPI 3010–17, UCM 39887, 41147, 44446–62); Lachiguirí (USNM 111473–74).

L. flavimaculatum

UNKNOWN: (0): Locality unknown (BMNH 1946.8.30.44). **VERACRUZ:** (1): 35 km SW Jesús Carranza (KU 26919); 25 km SE Jesús Carranza (KU 26920–21); 20 km E Jesús Carranza (KU 24453); (2): Río de las Playas (USNM 118638); (3): Catemaco: Colonia Adalberto Tejada (ENEPI 2104). **OAXACA:** (1): Río Mono Blanco, Juchitán (UIMNH 36832); (2): La Gloria (UIMNH 35515); (3): Mogoñé (UIMNH 40811); (4): 50.5 mi S Acazacan, Hwy 185 (TNHC 25182); Palomares, Juchitán (UCM 39888); 2.8 mi N Río Sarabia (UMMZ 115096); 2 mi S Toluca (KU 39676). **TOBASCO:** (1): Teapa (BMNH 1913.7.19.95, LACM 61260–61, LSUMZ 6878–79, UIMNH 47883, UMMZ 113777); (2): Soledad (UIMNH 47884); (3): Mpo. Tacotalpa: Cueva o Gruta Costachica (IBH 3676). **CHIAPAS:** (1): Ruinas de Palenque (EAL 3030–31, UF 32915–16, KU 94104–05); Palenque (LACM 65117–19); San Juanito, Palenque (USNM 111486–87); 6.5 km S Palenque (MZFC 4186); (2): 4.5 km S Pichucalco (KU 94106); (3): El Estoracan (ca 50 km N Cintalapa) (AMNH 73468); (4): Chiapa, 1 mi W (TNHC 27517–18); (5): 32 km NW Ocozocoautla, Selva del Ocote (JFC); 16.1 mi NW

Ocozocoautla (LACM 61259); 25 mi (by rd to Malpaso) NW Ocozocoautla (UAZ 28764, 28805–07); Ocozocoautla Selva El Ocote (MCZ 54321–22); 12 km N Berriozábal (MZFC 4134, UTEP 5365–66); 26 km N Ocozocoautla (UTEP 5367–68); (6): ca. 5 km S Solusuchiapa (UAZ 31635); (7): Lago Miramar, near San Quintín (JFC); (8): Lacanja (LACM 114244); (9): Rancho Alejandría Juárez (UCM 49275–79); (11): Salto del Agua: Cascada Misol-ja (IBH 3461); (12): Lago del Malpaso: Boca de Río de La Venta (ENEPI 3793). **QUINTANA ROO:** (1): 4.1 km NE Felipe Carrillo Puerto (UMRC 79-252). **BELIZE:** (1): Middlesex, near “Blue Hole” of Staum Creek (FMNH 4455); (2): State Forest, 4 m. from 12 m. Sta. on Staum Cr. R.R. (FMNH 4453–54); (3): Bokowina (BMNH 1973.2537–42, FMNH 49271–75); (4): Double Falls (FMNH 49276); (5): Baking Pot (MCZ 18953); (6): Toledo Dist.: ca. 1/2 mi from Village of Blue Creek (CM 117260); (7): Cayo: Xunantunich Ruins (KU 171679–80). **GUATEMALA:** (0): Province du Petén (Amer. centrale) (MNHN 782); (1): El Petén: 15 km NW Chinajá (KU 55864, 59552); Alta Verapaz: Chinajá (KU 59555); Río de Pasión, nr. Petén–Alta Verapaz border (UMMZ 79072); (2): Izabal: Quiriguá (CAS 68479–82, USNM 58384–85); (3): Petén: Piedras Negras (USNM 111475–83, UIMNH 48875); Desepeño (USNM 111484); (4): Alta Verapaz: Finca Volcán (UMMZ 91145–47); Finca Volcán, elev. 875 m, 25 km NW (by rd) Senahú (MVZ 159932–33). **HONDURAS:** (1): Dept. Cortés: Finca Fe, N Lago de Yojoa (LACM 45260); El Copito, 1 mi SE El Jaral (LACM 47831–33); 1 mi W El Jaral (LSUMZ 24217); Amapa Research Sta. (AMNH 70459); (2): Atlántida: mts above Corozal, 15 km E La Ceiba (LACM 47825–30, LSUMZ 21514–21); Piedra Pintada, 6.5 mi E La Ceiba (LACM 47834–35); (3): Olanchito: E.N.A., 4.5 km SE Catcamas (LACM 47823–24); (4): nr. Chamelecón (MCZ 29886–87); (5): Fortuna D.: Puerto Arturo (MCZ 21741); Tela: Port Town (MCZ 21814); Tela (MCZ 29394–95, USNM 94417–22, 101278); (6): Los Indios, Tela R.R. (FMNH 21788); Los Indios Farm, 76 km W Tela R.R. (MCZ 38903–22); Río Ulúa (UMMZ 77840); about 50 mi from Tela (FMNH 13002–03); (7): San Pedro, Montaña Santana (MCZ 29396); (8): Subirana Valley (MCZ 38901–02). **NICARAGUA:** (0): Nicaragua (MCZ 6250); (1): Río San Juan (USNM 19543); San Juan del Norte (USNM 15644); nr. Greytown (USNM 19739); (2): 10 mi above Recreo, Río Mico (UMMZ 79846); (3): Chontales, Tule Creek (AMNH 16402); (4): Departamento Río San Juan, appx. 15 km S El Castillo on north bank of the Río San Juan at Isla el Diamante (OMNH 38244–47). **COSTA RICA:** (0): Costa Rica (CAS 54645); (1): Limón Prov.: ca. 50 mi NW Limón, ca. 1.75 mi S mouth Río Tortuguero (AMNH 89257–8); SW face of Cerro Tortuguero (UF TC30, KC923); (2): Heredia Prov.: Finca La Selva, jct. of Río Viejo and Río Sarapiquí (CRE 483, 6300); E of Puerto Viejo

on La Selva field station, river road trail (UMMZ 145862); Puerto Viejo Sarapiquí (CRE 2890, KU 67382, 104079); 2 km S Puerto Viejo (CRE 2891); 1.5 km N Puerto Viejo (KU 67383–5); 9.7 km (by rd) W Puerto Viejo (LACM 128534–54); 13 km (by rd to Guápiles) SSE Puerto Viejo (LACM 128555–59); 10 km WSW Puerto Viejo Sarapiquí (MVZ 217606); (5): Lower Reventazón River, La Castilla (ANSP 23682); (6): Limón Prov.: La Lola, Experimental Cacao Finca of I.I.C.A. (CRE 500); Batán (KU 34210); La Lola, ca. 4 mi W Batán (KU 34211–12, 34214–16); (7): Cartago Prov.: Turrialba: S. Bank of Reventazón (CRE 504); Morehouse Finca, 5 mi S Turrialba (KU 34208); (8): Guanacaste Prov.: El Silencio (CRE 3057); San Bosco (CRE 6282, FMNH 176530); 4–5 km NNE Tilarán (KU 36250); Lago de Arenal (KU 102446–48); 2.5 km W Tilarán (CRE 734); Tilarán (UF 33137); 2 km E Arenal along rd to Tilarán (LACM 137499, UMMZ 137543); (9): Alajuela Prov.: 11 mi N Florencia (CRE 2624); 5 mi N of Quesada (CRE 7156); (14): Limón Prov.: 1 1/2 mi E of Los Diamantes (CRE 8049); Los Diamantes, Guápiles (KU 34205–7, 34213); (16): Guanacaste: Tenorio, Los Flores, Las Cañas (KU 34217–19); (17): Limón Prov.: Suretka, (KU 36251–55); (18): Limón Prov.: Puerto Viejo (KU 36256–57); (19): Alajuela Prov.: Poco Sol, San Carlos drainage (LACM 114858); (21): Limón Prov.: La Colonia, 23 km NE Guápiles (MVZ 82876); (22): Limón Prov.: ca. 29 km (air) W Tortuguero (LACM 131067–111, 132392); (23): La Emilia (ANSP 21403); (24): Puerto Viejo (LACM 115744–45). PANAMÁ: (1): Canal Zone: 3 mi SE Achiotte (Colón Prov.) (UF 32919–22, 32924–48, UAZ 27637–44, 28610–18, 28826–27, 31777); 8 mi (air line) NNW Escobal (LACM 128560–87, 131149); (2): Canal Zone: Barro Colorado Id. (AMNH 75985, ANSP 21089–90, 23024, 24579–80, CAS 93853, CM 6638, FMNH 13374, KU 80524, MCZ 18861, UMMZ 61611); (3): Panamá: Chilibrillo Cave “c” (AMNH 71688–89, FMNH 60161); Chilibrillo Cave, near Chilibre (KU 113496–97); Canal Zone: Chilibre Bat Caves near Chagres River on Madden Dam Rd (SDSNH 5697); Chilibrillo River (MCZ 17747); (4): Canal Zone: vic. George Green Park, 3 mi (air line) NE Summit (UAZ 28607–09); (5): Colón: Santa Rita Lumber Rd, nr. Agua Clara (MCZ 133640); (6): Panamá Prov.: N base Cerro Trinidad, El Aguacate (UF 32923); (7): Ciricito (CAS 71470); (8): Cabi-ma, Pacific slope (USNM 48503); (9): Bocas de Toro: ca. 5 km W Almirante (AMNH 107589); 4.8 km W Almirante (KU 96924); 12.8 km W Almirante (KU 96925); 12 mi W of Almirante (USNM 65809); Almirante (USNM 193444).

L. gaigeae

QUERÉTARO: (1): 4 mi SW El Lobo (BCB 68-720, 774–779); 2.8 mi W El Madroño, 11.9 mi W Xilitla (CU 9690–91); 0.6 mi N of Mex 120 on dirt rd to Tres Lagunas, 0.8 mi W El Madroño (CU

9684–86, 9770–71); 4.1 mi SW El Lobo (UF 28331–52); 2.2 mi (by Hwy 120) SW El Madroño (LACM 106770); 3.5 mi (by rd) W El Lobo (LACM 106807–09, 127169–70); N of Mex Hwy 120, nr El Lobo (MVZ 111459); 2.2 mi SW El Lobo (SAM 1105); 2.2 mi W Madroños (TCWC 27790–829); 3.2 mi W El Lobo (TCWC 29619, 29650–82, 30664–74, 35665–66); 2.4 mi W El Madroño (TCWC 29620–32, 29634–40, 29642, 29644–47, 29649, 29683–90); 4.9 mi W El Madroño (TCWC 29633); 2.4 mi W, 1 mi S El Madroño (TCWC 29648, 29643); 3.2 mi W, 2.3 mi S El Lobo (TCWC 30675); 3.2 mi W, 1 mi S El Lobo (TCWC 30676); 3.8 mi W El Lobo (TCWC 32292–93, 32296–363, 33052–62); 0.9 mi E El Lobo (TCWC 32294); 3.8 mi W, 1.8 mi S El Lobo (TCWC 38608–10); El Lobo (TCWC 45511–18, 45521–24, 45633–34); (2): 3 mi E Jalpan (TCWC 35608–10); 6 mi E Jalpan (TCWC 35611–64); 2 mi NE Jalpan (UMMZ 129746); (3): 10.2 mi W San Joaquín (LACM 109153, TCWC 40686–87, 40975); vic Lizaro Vega, 7.5 mi (by rd) N jct. Mex 120 on San Joaquín Rd (TCWC 53024); (4): 8.5 mi S Arroyo Seco (TCWC 32364); 3.7 mi S Arroyo Seco (TCWC 37677–79); 1 mi S Arroyo Seco (TCWC 38611); (5): 5.7 mi (by rd) E Tilaco, ca. 1 mi W Santa Inéz (CSL 6863–64); 5.2 mi (by Tilaco Rd) S La Lagunita (LACM 127065–66, 127343–46, 127418–20, 131143); (7): 16.4 mi E Landa de Matamoros (TCWC 29641); 15.5 mi E Landa de Matamoros (TCWC 32295). HIDALGO: (1): La Placita, 8 km S Jacala (UIMNH 26180–210); (2): Durango (AMNH 66063, 100769–70, FMNH 25885, KU 70550–51, MCZ 42145–48, UAZ 28880–915, UCM 49849–50, UIMNH 26220–23, 48010–11, USNM 111471, USNM 80951); 2 mi N Durango, 13 mi (by Mex 85) S Jacala (AMNH 100768, UAZ 28865–79); nr Minas Viejas (CAS-SU 13879, UIMNH 26211–19); 21 mi N Zimapan on Mex 85 (LACM 67530–34); 4 mi N Durango, 11 mi (by Mex 85) S Jacala (UAZ 28862–64).

L. lipetzi

CHIAPAS: (1): Lago de Mal Paso, headwaters of Río de La Venta, 30 km N Cintalapa (UCM 51425); Lago de Malpaso, Boca de Río de La Venta (ENEPI 3792).

L. lineri

OAXACA: (1): Cafetal El Pacífico, 2.1 mi N and 0.4 mi E Candelaria Loxicha on trail to Cafetal Hedweges (LACM 134844, UCM 48452); (2): Cafetal “Alemania” (AMNH 15977).

L. lowei

OAXACA: (1): Zoogocho (IPN 5671–72); 4.0 km (by rd) SE San Bartolomé Zoogocho (ENEPI 3732–33, 3804–07, IBH 7497–7500, LACM 143732–33); 5.8 km (by rd) S San Bartolomé Zoogocho (ENEPI 3738); 1.0 km SE San Bartolomé Zoogocho (ENEPI 3739).

L. mayae

GUATEMALA: (1): Alta Verapaz: Chinajá (KU 55863, 59553–54, 59556–59, LACM 75194–95); (2): Vera Paz (NMBA 3751); (3): Huehuetenango: Finca Yulaxac, 15 km N Barillas (MVZ 134702); Finca Chiblac, 12 km NE Barillas (MVZ 143448–49, 161798); Sierra de los Cuchumatanes, Finca Chiblac, 4.4 km (by rd) S Casa Grande on rd to “La Galera” (UTA R-38021); Finca Chiblac, ca. 22.0 km NNE Barillas (UTA R-38022–23); (4): Finca Volcán, 25 km NW (by rd) Senahú, Alta Verapaz (MVZ 159931).

L. micropholis

TAMAULIPAS: (0): cave (TTU R-7311); (1): Cave at El Pachón, ca. 5 mi NNE Antigua Morelos (LACM 106767–68, 136369–70, UAZ 28762, 28767–69, UIMNH 37296, UMMZ 101298–99, 102886–88); 11.3 mi S Ciudad Mante, Hwy 85 (TCWC 57256); (2): 1.5 mi SW Quintero (AMNH 93409); Gruta de Quintero (LACM 66662, SAM 885). SAN LUIS POTOSÍ: (1): 6 mi E Valles (BCB 13837–42); (2): 5.4 mi S, 1.4 mi E Valles (TCWC 60621, 60766–69, 60836).

L. occulor

SAN LUIS POTOSÍ: (1): Hda. Capulín (LSUMZ 2379–80); (2): Tamán (ENEPI 2946). QUERÉTA-RO: (1): Jalpan (USNM 47133–35); (2): 2.5 mi S Conca, Hda. Conca (TCWC 35605–06, 48499); (3): 1.5 mi E Landa (TCWC 33063); 1.2 mi E Landa de Matamoros (TCWC 29691).

L. pajapanense

VERACRUZ: (1): SE slope Volcán San Martín Pajapán (FMNH 78382); SE slope Volcán San Martín (KU 97290, UMMZ 126362); S slope Volcán San Martín (LACM 135510, UMMZ 118220); Colonia de Bastonal, above Quezalapam (TCWC 19133); 4 mi SE Tebanca (TCWC 21364); 1 mi NW Sontecomapan (TCWC 21365); Univ. Mex. Biol. Exp. Sta. ca. 33 km ENE Catemaco (TCWC 53351); Coyame, 9 mi (by rd) SE Catemaco (UAZ 28804); 2 mi (by rd) SE Sontecomapan, 14 mi (by rd) NE Catemaco (UAZ 28808–11, 28765); Laguna Catemaco, nr Cuezalapam (UMMZ 126363–64); 2.1 mi NW (by rd) Sontecomapan (UTAR 3107, 3110, 3116); (2): 35 km SE Jesús Carranza (KU 26913); (3): Mpo. Huayacocotla: San Antonio, Ixtatetla (LACM 137605).

L. radula

OAXACA: (1): San José Manteca (USNM 111472).

L. reticulatum

COSTA RICA: (0): Pacific coast (KU 34209); (3): Puntarenas Prov.: Coto, km 47 on rail to Golfito (CRE 178); (4): San José Prov.: 6 km ESE San Isidro

del General (CRE 666); 2 mi E San Isidro del General (KU 34189–93); 10–12 mi WSW San Isidro del General (KU 34194–202, 34204); 8.8 mi SW San Isidro del General (UMMZ 117474); 7.3 mi SW San Isidro del General (UMMZ 11475); (11): Puntarenas Prov.: 2 km SSW Cañas Gordas (CRE 7227); Agua Buena (KU 36238–49, 56064); Finca Loma Linda (ca 2 km SW of Cañas Gordas) (UMMZ 128639); (12): Puntarenas Prov.: 4 mi S San Vito de Java near Wilson's Finca (CRE 3119); 6 km S San Vito de Java (LACM 72323); San Vito: ca. 1 mi SW Finca Las Cruces (LACM 76160–62, 76164–70); Copal: 4.5 mi SSE San Vito, vic. S Las Cruces (LACM 76163); jct. rd to Río Java & San Vito-Agua Buena Rd, 1 mi S Las Cruces (LACM 106794); (13): Puntarenas Prov.: 1 and 7/8 mi SW of Rincón de Osa (CRE 7237); 6 km SSW Rincón (CRE 3158); 4.5 km W Rincón de Osa (KU 102449–50); (15): San José Prov.: Salitral de Santa Ana (CRE 229); (25): Guanacaste Prov.: 4–5 km NNE Tilarán (KU 36230–37).

L. smithii

GUERRERO: (1): 2 km W Puerto Marqués (CU 9676–79, 9692–93, 9772); 2.5 km W Puerto Marqués (IBH 1651, 2243–45); 1 km (airline) NW Puerto Marqués (LACM 128590, 130027–29). VERACRUZ: 2 mi NW Sontecomapan (TCWC 26716). OAXACA: (0): Tehuantepec (MNH 76.95, 4323, A4323, B4323); (1): 3 mi NW Tehuantepec (KU 38026–28); 6 mi WNW Tehuantepec, Río Tejas (KU 42289); 8.2 mi (by Hwy 190) WNW Tehuantepec (LACM 128588–89, 130030–32); nr Tehuantepec (MCZ 66974, USNM 46998, 47000); Tehuantepec (UIMNH 40745); Cerro Guiengola, 1/2 way up (FMNH 106312–15); Cerro Guiengola (UIMNH 26231–32); Quiengola Mt., 8 km NW Tehuantepec (UMMZ 82419–22); Cerro Arenal (USNM 111488); (2): 39 mi SW Cintalapa (BCB 13400); 6 mi SE Tapanatepec (KU 42290); 2.7 mi E Tapanatepec (KU 75585); 95 mi N Tuxtla Gutiérrez (LACM 100671); Municipio de Juchitán: 3.2 km NE Tapanatepec (LACM 134468–76, 136677); Tapanatepec (MCZ 27900); 1.5 mi (by Mex 190) E Tapanatepec (UAZ 28794, 30279); Río Novillero, 2.7 mi N Tapanatepec (UIMNH 83160); 3 mi SW of Chiapas border (UMMZ 118721); Santa Efigenia (USNM 46687); (3): Rincón Bamba (UIMNH 35514, 35528); Rincón Bamba (UIMNH 37348); (5): 2 mi S La Ventosa (UIMNH 42835–36); (6): 7.7 mi SE Camarón (UMMZ 115097); Portillo Nejapa (AMNH 98120); (9): Cerro Atravesado, El Palmar (AMNH 66890, 66955); (11): along Oaxaca–Puerto Escondido Rd., km [?] S of Oaxaca (CAS 101381); along Oaxaca–Puerto Escondido Rd., km 233 S of Oaxaca (CAS 101383); (13): El Limón (USNM 111490); (15): Tres Cruces (FMNH 100570, USNM 111489); La Concepción (USNM 111491–92); (17): 29 mi W Tapanatepec (BCB 13397–99); (18): Santo Domingo de Guzmán (BMNH 90.10.10.2); Mts nr Santo Domingo

(USNM 48105). **CHIAPAS:** (1): 9 mi (by Mex 200) NW Escuintla (AMNH 100767, 102295, UAZ 28797–802); La Esperanza (CAS-SU 13877; FMNH 123942–55, 124937–52, 125127–31, 178164–77, MCZ 46786–91, UCM 39685, UIMNH 10952–11005, USNM 111499–523); 30 mi NW Huixtla, Hwy 200 (LACM 100666–70, 101263); Cerro Ovando (LACM 135511); 2.5 mi (by rd) NE Acacoyaga (LACM 136359–64); 14 mi SE Mapastepec (TCWC 55523); 15.3 mi SE Mapastepec, Hwy 200 (TCWC 57502, 57504); 14 mi (by Mex 200) NW Escuintla (UAZ 28783–87, 28803); 2–3 km E (rd) El Triunfo (MVZ 191448–49); 4 mi NW Mapastepec, 24 mi (by Mex 200) NW Escuintla (UAZ 28795, 28812–17); 4 mi (by Mex 200) NW Escuintla (UAZ 28796); ca. 1/2 mi (by Mex 200) NW Escuintla (UAZ 28788–93); Region Soconusco (UIMNH 33604–05); Dist. Soconusco, 6 km NE Escuintla (UMMZ 87251–54, 87257–300, 87303–22); Dist. Soconusco, vic Escuintla (UMMZ 88289, 88313); lake nr Acacoyagua (USNM 111493–96); La Magnolia, 8 km NW La Esperanza (USNM 111497); (2): Tonolá (FMNH 106949, 106951–52, 179365, USNM 111498); 15 mi (by Mex 200) SE Tonolá (UAZ 28766); Nr Tonolá (UIMNH 26226–29); (3): 6.8 mi N Arriaga (EAL 1746); 9.5 mi NE Arriaga (LACM 61258); crest above Arriaga (UMMZ 94825); (4): “km 945” between Tapanatepec and Las Cruces on Mex Hwy 190 (UMMZ 126867); (5): near Asunción (FMNH 106950, 106953). **GUATEMALA:** (28): (0): Guatemala occidental (MNH 4968, A4968); (1): Escuintla: Escuintla (CAS 71914); Finca El Zapote (FMNH 57032); Finca El Salto, 2 km E Escuintla (MVZ 88420, 88422–23, 93174, 98023–24, 104181); 10 km N Escuintla, Finca Vista Hermosa (UMMZ 127839–40); (2): Finca San Carlos Miramar, 12.5 km SW Yepocapa (by rd), Chimaltenango (MVZ 88426); (3): 1 mi SE Monogoy, Jutiapa (KU 42288); (4): Depto Jutiapa: Finca La Trinidad (UMMZ 107646–51); (5): Depto. Santa Rosa: Finca El Cahuito (UMMZ 107070); 7 mi W Taxisco, “Km 99” near Cartago no. 1 bridge (UMMZ 126931); (6): Depto. Santa Rosa: Finca La Gloria (UMMZ 118263); (7): 10 mi N Chicacao, Suchitepéquez (UIMNH 46514–15); (8): Suchitepéquez: Mazatenango (CAS 68484–86, 68488–89, 68491–504, CM 39734, NMBA 3750, 3748–49, 3752, 8039–40); (9): Suchitepéquez: Volcán Zunil (CAS 68505–06, 68483); (11): Sololá, Finca Olas de Mocá (AMNH 43225). **EL SALVADOR:** (1): Dept. Sonsonate: Hacienda Chilata (MVZ 40071–73).

L. sylvaticum

NUEVO LEÓN: (1): La Boca (KU 92612–13); ca. 7 km NE Santiago, Presa La Boca (LACM 106781–92); (2): 5 mi N Las Ajuntas (EAL 4644); (3): San Roque, ca. 6 km S Cerro de la Silla (LACM 138179–80). **TAMAULIPAS:** (1): Rancho del Cielo [and vic.], ca. 5 mi NW Gómez Farías (AMNH

107273, BMNH 1958.1.2.40, LACM 106751–56, UIMNH 37295, UMMZ 101301, 101374–75, 102978–81, 109763–64); El Elephante, ca. 7 km (airline) W Gómez Farías (LACM 106757–60); Jullilo, 12.7 km (airline) NW Gómez Farías (LACM 106762–65); W Rancho del Cielo (LSUMZ 10989); Gómez Farías–La Joya de Salas trail at 4600 ft. (UMMZ 102977); Gómez Farías–La Joya de Salas trail below Agua Zarca (UMMZ 109765); 2.5 mi ESE La Joya (UMMZ 109766); cloud forest above Encino (TCWC 65549); (2): 10 mi W, 2 mi S Piedra (KU 33993–94); Sierra de Tamaulipas, Santa María (UMMZ 102889–90); (3): 8 mi S, 6 mi W Victorio, Sierra Madre Oriental (KU 33992). **SAN LUIS POTOSÍ:** (1): Álvarez (58 kilo) (MCZ 24507–08); between San Francisco and Álvarez (MCZ 157826); Valle de los Fantasmos (SDSNH 60482); (3): Buenavista (20 mi NE Cerritos) (AMNH 64025); (4): 27 km (by Mex 80) W El Naranjo (LACM 131145–48); 3.8 mi (by Hwy 80) NNE Ciudad del Maíz (LACM 131144); 5 mi NE Ciudad del Maíz (TCWC 35582); (5): Huichihuayan (FMNH 39631). **QUERÉTARO:** (1): El Madroño, 3.5 mi W (rd) El Lobo (LACM 109771); 3.5 mi SW El Lobo (SAM 1104); 2.4 mi W El Madroño (TCWC 29692–95, 29701–07); 1.1 mi S El Madroño (TCWC 29696); 2.4 mi W, 1 mi S El Madroño (TCWC 29697); 2.4 mi W, 1.8 mi S El Madroño (TCWC 29698–700); 3.8 mi W El Lobo (TCWC 32291, 33064); 3.2 mi W El Lobo (TCWC 35607); 2 mi SW El Lobo (UMMZ 129749); (2): Mpo. Pinal de Amoles: 1 km S Pinal de Amoles (IBH 4060). **HIDALGO:** (1): 7 mi N Zacualtipán (FMNH 100102, 100356, 100411); 4.0 mi (by Hwy 105) S Tianquistengo (LACM 106721); 5.8 mi (by Hwy 105) S Tianquistengo (LACM 106741–48, 136365–68); 3 mi S Tianquistengo (UIMNH 26230). **VERACRUZ:** (1): 4 km W Tlapacoyam (KU 26909); (2): Alvarado Mpo.: Ciudad de Alvarado (MZFC 1722).

L. tarascae

MICHOACÁN: (1): Aguila District, near Mexiquillo (IPN 9221–22; LACM 134226); (2): Aguilla Mpo.: Río Chilitos Cañón, Cueva La Virgen (MZFC 8603).

L. tuxtlae

VERACRUZ: (1): Sontecomapan (CM 41470); Coxoapan (Sontecomapan) (UF 32914); Montepio (UF 32917); 18 mi NNE Catemaco (JCL 67); South slope Volcán San Martín Tuxtla (KU 59560); E of Lago Catemaco, 12.7 mi from Catemaco by rd (LACM 106795); ca. 5 mi N Catemaco off rd to Sontecomapan (LACM 134845); 12.9 mi (by rd) NNW Sontecomapan (LACM 136352–58); forest above Playa Escondida, 30 km NNE Catemaco (MVZ 171872); Salto de Eyipantla, Eyipantla (TCWC 19134); 1 mi W Sontecomapan (TCWC 19135); lower falls on Río Quezalapam, Quezalapam (TCWC 19136); Colonia de Bastonal (TCWC

19137); 4 mi SE Tebanca (TCWC 21366); Río Quezalapan, 1 mi E Lago Catemaco (TCWC 21367); Río Quezalapan, 2 mi E Lago Catemaco (TCWC 21368–69); Dos Arroyos, 5 mi E Zapopan (TCWC 21370–71); Volcán San Martín (TCWC 22102–03); 2 mi NW Sontecomapan (TCWC 26717); Volcán San Martín E lower slope (TNHC 29792–93); Univ. Mex. Bio. Exp. Sta., ca. 33 km ENE Catemaco (TCWC 53352–53); Coyame, 9 mi (by rd) SE Catemaco (UAZ 28763); 2 mi (by rd) SE Sontecomapan, 14 mi (by rd) NE Catemaco (UAZ 28770–79); San Martín Mt., El Tular Sta. (UIMNH 35449); San Martín Mt. (UIMNH 35463–64); Rancho El Tular, ca. 5 mi N San Andrés Tuxtla (UIMNH 40285); Volcán San Martín (UIMNH 67064, 80695–99); Río Tecolapan, 2.4 mi NNW Tapalapan (UMMZ 115098–99); S slope Volcán San Martín (UMMZ 118219); midway between Coyame-Tebanca along shore Laguna Catemaco (UMMZ 121164); SE slope, Volcán San Martín (UMMZ 121165, 122112, 126360–61); between Laguna Catemaco and Volcán San Martín (UMMZ 121166); Rancho El Tular, 15 mi N San Andrés Tuxtla (USNM 139731); 2.1 mi NW (by rd) Sontecomapan (UTAR 3101, 3103, 3104, 3108, 3109, 3111–13, 3115); 2.5 mi SSW Sontecomapan (UTAR 3127); ca. 3 mi E of Cuetzalapan (UTAR 3133); Río Cuetzalapan S of Tebanca (UTAR 3139–40); 5.6 mi ESE Tebanca (UTAR 3156); 7.7 mi NW Sontecomapan (UTAR 3728–30, 3733–34); (2): 25 km SE Jesús Carranza (KU 26912). **OAXACA:** (1): Vista Hermosa (KU 87396–98, UCM 49280); 30 mi (by rd) NE Llano de las Flores (UMMZ 125870); Valle Nacional Mpo.: alrededores de Metates, Sierra Juárez (MZFC 2262); (2): Mts nr La Gloria (UIMNH 37236); (3): Finca San Carlos, Matías Romero Oaxaca, Río Coatzacoalcas, at the mouth of Río Sarabia (UF 32918). **CHIAPAS:** (1): 43 km on rd between Ocozocoautla and Malpasos (UCM 49281); 25 mi (by rd to Malpasos) NW Ocozocoautla (UAZ 28780–82).

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